ECOLOGICAL MONOGRAPHS

VOLUME 14 APRIL, 1944 NUMBER 2

THE NATURAL VEGETATION OF THE ISLAND OF TOBAGO, BRITISH WEST INDIES

J. S. BEARD
Colonial Forest Service, Trinidad and Tobago

TABLE OF CONTENTS

THE NATURAL VEGETATION OF THE ISLAND OF TOBAGO, BRITISH WEST INDIES

GROUNDWORK

The little West Indian island of Tobago, in contrast to its rich aunt Trinidad, has hitherto had practically no attention paid to ecological study of its vegetation. Ecological work has been limited to two short enumeration traverses run respectively by Forest Officers R. L. Brooks in 1932 and C. Swabey in 1933. Based on the data so provided, R. C. Marshall in his "Physiography and Vegetation of Trinidad and Tobago" (1934) described a "Crappo-Duckwood association (Carapa-Ocotea)" for Tobago as a climatic climax association under tropical rain forest and a "Galba-Balata type (Calophyllum-Mimusops)" which he considered to be a "deflected climax." The descriptions are quite short, consisting of little more than the names of the more important component species, for as the author states, "the vegetation of Tobago needs further study and there is little doubt that this will bring to light more than one association."

Fortunately, while the vegetation has received scant notice as vegetation, that is, ecologically, it has been well studied floristically: again, not so thoroughly as in Trinidad, but sufficiently so that "the flora of all regions except that of the Forest Reserve of the Main Ridge may now be regarded as comparatively well-known" (Sandwith 1938). The principal collecting was done by the late W. E. Broadway between 1908 and 1933. Other prominent contributors were R. O. Williams and E. E. Cheesman (authors of the "Flora of Trinidad and Tobago"), W. G. Freeman, and N. Y. Sandwith. Collections of forest trees have been contributed by R. C. Marshall, R. L. Brooks and C. Swabey. A considerable portion of the flora of Tobago has been dealt with in the published parts of the "Flora of Trinidad and Tobago," in Sandwith's "Notes on the Flora of Tobago" (1938) and in Broadway's "The Palms of Tobago" (1916). The writer has had access in addition to an unpublished paper by C. Swabey on "The Palms of Trinidad and Tobago." Grateful acknowledgment is made to all those above mentioned for the data which served as the groundwork for the present vegetation-study.

The work here described was confined to natural or more or less natural vegetation: that is to say, to those areas of virgin forest, woodland, and swamp which have not yet been destroyed or radically altered by human interference. These comprise the Forest Reserve on the Main Ridge and adjoining blocks of Crown Lands (in all about 14,570 acres), the small island of Little Tobago off the northeast coast, some small mangrove swamps and patches of littoral scrub. The remainder of the island has been so thoroughly cleared of forest that it is now difficult or almost impossible to reconstruct a picture of it. It will be seen that the forests of the Main Ridge, that is, of the mountainous and inaccessible interior, comprise by far the larger part of the vegetation studied, and here botanical collections have been least comprehensive. As Sandwith (1938) remarks, ". . . the impression gained is that there is a great deal more work to be done in what is, obviously, the most interesting and important region in the island, the Forest Reserve of the Main Ridge. . . . It is quite evident that repeated exploration of these forests will add many new trees, herbs and ferns to the known flora of the island." Little difficulty was experienced by the writer in identifying the trees and shrubs noted on Little Tobago and in littoral and mangrove areas, but a certain amount of trouble was encountered on the Main Ridge.

The writer was able to pay a visit of two weeks to Tobago from February 21 to March 7, 1942 as part of his duties as Assistant Conservator of Forests. The first and last named days being occupied by travelling, 13 working days were available, of which one day was spent examining littoral and mangrove vegetation, one day on Little Tobago and 11 days on the Main Ridge.

In examining the littoral and mangrove vegetation and also that of Little Tobago, the areas observed were relatively small and more or less the whole could be looked at and generally examined. General notes were taken of the species found, of their estimated relative frequency and of any other relevant data. Any unknown species were collected and photographs taken to show characteristic features of the vegetation. In studying the forests of the Main Ridge the large size of the area, the doubtful scope of botanical knowledge and the broken, inaccessible nature of the country were more formidable problems. Tobago is not an island well provided with motor roads. It is possible to drive all along the windward coast but the north side must be reached by sea, on horse, or afoot. In any case no driving road even approaches the Forest Reserve. The latter is traversed by two well-graded mule paths and a number of others run up to its boundaries. Using a map, a program was drawn up for the eleven available days aiming at covering as much ground as possible within the forest by utilizing all the available points of access. This was carried out as follows, the forest being entered from the St. George-Castara Road on 3 days, the Cardiff Road on 2 days, the Pulteney Hill Road on 1 day, the Roxborough-Parlatuvier Road on 2 days, the Louis d'or Road on 1 day, the Pigeon Hill Road on 1 day, and the Northside Road on 1 day from two different points.

The method of the enumeration traverse was employed as the basis of field work. The writer was

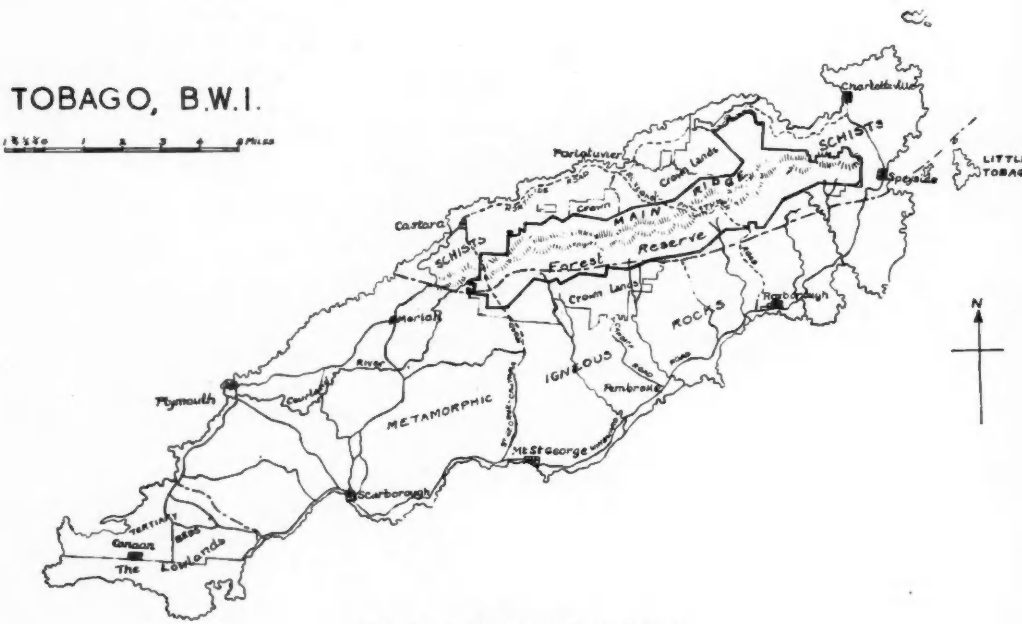

FIG. 1. Geological map of Tobago.

accompanied by two local woodcutters who had a fair knowledge of the local names of trees and who were accustomed to recognize the trees commonly cut for timber. They absorbed the idea of the enumeration fairly rapidly and after a couple of days became skilled in the work. On arriving at the point where it had been decided to run a traverse, a line was roughly set with a pocket compass and followed through by the same means, cutlassing passage where necessary. Lines were not cut in advance for enumeration and were not dead true on a bearing or straight or accurately measured. The length of each traverse was estimated subsequently by checking the measured length obtained from plotting on the map the points of beginning and ending against the number of trees recorded, since experience elsewhere had suggested the average number of trees to expect per acre in each type of forest. Working with a good topographic map at 1:50,000, in mountainous country, the writer found this method quite satisfactory.

In traversing the line the local name of every tree over 1 foot girth within ½ chain on either side of the line was called with its estimated girth and booked. In this way every 10 chains of traverse represents 10 square chains or 1 acre enumerated. At the same time notes were taken on ground vegetation, epiphytes, structure, soil types and other data of importance. In cases where a tree was known to the writer a note was taken correlating its botanical name with the local name given. Where the local name was of a tree not certainly known to the writer, leaves were collected and flowers if available. If the tree had no local name, that is was not known to the local men either, it was collected and was given a descriptive name such as "Stringybark," careful note being taken of its bark and blaze characters so that it would be recognized again. Specimens of 85 different species were collected in this way and brought back to Trinidad. Only a small proportion of these, unfortunately, possessed flowers or fruit. Seventy-one of them were, however, subsequently identified, most of them with certainty, in the Herbarium in Port of Spain. Of the remaining 14, 6 were subsequently named at the New York Botanical Garden.

Soil borings were made from time to time on the traverses, and two profiles considered typical of two main soil types distinguished were described and sampled. Similarly, once it became clear that two distinct plant formations existed on the Main Ridge, a sample forest profile was selected and measured in each. In each case a strip of forest 100 feet x 25 feet was selected as showing structure considered typical of the formation and was felled out and measured.

FACTORS OF THE ENVIRONMENT

PHYSIOGRAPHY

Tobago is an island having an area of some 114 square miles and lies in the Atlantic separated about 26 miles from the northeastern point of Trinidad between the latter island and Barbados and Grenada, southernmost of the Lesser Antilles. Structurally it is not related to the Antilles, but is in agreement with the neighboring portion of the South-American continent and is therefore mountainous with a central east-west backbone. The island itself is 26 miles in length and 7½ miles broad at its widest point, being roughly elliptical in shape with the main axis of the ellipse inclined at 30° to the east-west latitudes. The mountain backbone known as the Main Ridge is a chain tending 15° to east-west latitudes, that is, running slightly crosswise of the island, and is some 10 miles long, rising abruptly at either end. The highest point of the Main Ridge touches 1,890 feet, not in any well-defined peak, the crests running as a ridge about 1,600 to 1,700 feet high throughout. The adjacent country is all steeply broken land, a jumble of sharp ridges and deep gullies and there is no coastal plain except at the southwestern extremity where the country gradually evens off to form a flat plain known as the Lowlands some 10 square miles in area. Topography in general is young and drainage is by swift-flowing torrents rising in the Main Ridge.

CLIMATE

The climate of Tobago differs slightly from that of the main part of Trinidad but is similar to that of the Toco district of the latter island, which is the part of Trinidad nearest to Tobago. To one accustomed to Trinidad there is a curiously different and more bracing "feel" to the air in Toco and Tobago: this may be connected with the constancy and force of the wind or with humidity. The climatic difference can be measured in rainfall, Toco and Tobago having a regime with maximum precipitation in November and the remainder of Trinidad in August.

RAINFALL

Due to the mountainous nature of the island, the rainfall varies rather widely from point to point. Table 1 shows a summary of records which have been kept at six different stations for periods of from 11 to 31 years. It will be seen that the average rainfall varies from 56.19 inches at the Government Farm in the southwest to 93.08 inches at Hermitage in the northeast. It is clear also that precipitation is by no means annually constant, the record driest and wettest years having a total at the Government Farm of 31.42 and 130.64 inches, respectively, and at Hermitage of 68.62 and 132.56 inches, respectively.

All the stations (Fig. 3) reveal a similar rainfall regime divided into a dry and a wet season, the former from January to May and the latter from June to December. There is a slight diminution of rainfall in October, showing a faint influence of the continental Guianese regime to the southward where the year is divided into two wet and two dry seasons. This phenomenon is scarcely appreciable in Tobago, however, being nothing like as distinct as in Trinidad. Climatically, Tobago belongs to the Lesser Antilles.

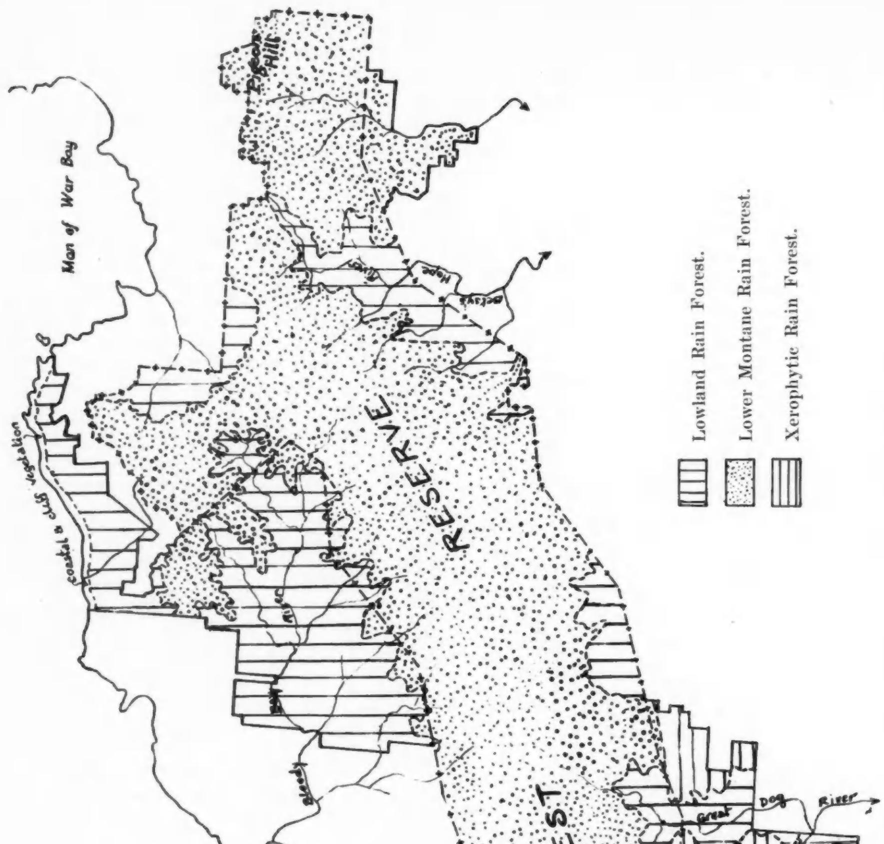

Fig. 2. Map showing the distribution of forest types on the Main Ridge of Tobago.

The seasonal drought revealed by the records is of comparatively extreme severity. Even at the wettest station, Hermitage, there are on the average three months with less than 4 inches of rain, that is, in which evaporation may be assumed to exceed precipitation. At the Government Farm there are five such months.

When considering the rainfall, as shown from records, in relation to the natural vegetation, one meets the difficulty that all the stations are located at Estates round the coast and that there are none on the Main Ridge. It can be established that the coastal lands are exposed to a climatic regime with seasonal drought of from three to five months, but it is clear that the high, mountainous interior is somewhat differently watered. As with all such mountainous islands, the high ground catches a large quantity of rain while the coastal lowlands both to the windward and to leeward may be commonly quite arid. In the case of a large, high island like Puerto Rico, for example, there is an alternation from the most hygrophilous rain forest to cactus desert. Similarly in Tobago the vegetation of the Main Ridge leads one to expect both a higher and better distributed rainfall than on the coast. The writer worked in these forests in late February and early March—the driest time of the year: the soil was quite moist throughout and a heavy rain shower fell on one day; whereas coastally the ground was dry and parched and no rain fell. In the writer's opinion it would be safe to assume an annual rainfall of at least 150 inches for the Main Ridge, no month having less than 4 inches.

TEMPERATURE AND HUMIDITY

No meteorological data of this kind appear to be available for Tobago. In Port of Spain, Trinidad, about 60 miles to the southwest, the mean annual temperature is about 78° F. varying between about 65° F. and 90° F., and relative humidity is always high, seldom below 60 percent in the daytime and approaching saturation at night or in the day after rain. Temperatures for Tobago are probably very similar, but humidity may possibly be lower.

WIND AND SUNSHINE

The prevailing wind is the northeast Trade, which blows with considerable constancy of force and direction. There are no available data as to velocity, but this probably exceeds 6 miles per hour at any time, being higher in the dry season. The presence of a fresh, constant breeze is a noticeable feature of the Main Ridge, even when in dense forest. Wind velocity may frequently increase considerably just before a rainstorm, doing much damage to tree growth in exposed places. Tobago is outside the hurricane zone, but has been visited by one hurricane in historical times, in 1847, when considerable damage was done.

Hours of sunshine probably average about 6 per day.

GEOLOGY

Two reports exist on the Geology of the island, a general review by Cunningham-Craig (1907) and a study of the Tertiary and Quaternary beds by Trechmann (1934).

Tobago lies on the same continental shelf which also carries Trinidad, being separated from the latter island by relatively shallow water whereas deeps of several hundred fathoms divide it from Barbados and Grenada. The mountains of Tobago constitute the last and most easterly link in the great coastal cordillera of Venezuela. Tobago, the Northern Range of Trinidad, and the Paria Peninsula of Venezuela are three ridges of related structure arranged parallel and *en echelon.*

The geological data on the accompanying map are based on Cunningham-Craig, the boundary between igneous and sedimentary rocks being corrected inside the Forest Reserve according to the writer's own observations. The whole of the island north of a rough line running parallel to and about a mile south of the Main Ridge is formed of metamorphic rocks of sedimentary origin consisting chiefly of schistose grits, often very felspathic, with talcose and talc-mica shists. These resemble in a general degree strata in the Northern Range of Trinidad and are most likely of similar age, that is, lower cretaceous: but limestones are totally absent and quartz veins relatively rare. The flat plain of the lowlands is composed of Tertiary and Quaternary beds, mainly coral limestones which rise in a series of flat terraces. The remainder of the island is formed of a mass of basic igneous rock which has shared the metamorphism of the schists and grits and is highly shattered. It appears to have been originally intrusive and agrees with the similar patch of igneous rock at Sans Souci in Trinidad.

The schists appear to have been laid down in open sea and derived from the erosion of land lying to the northward. During late Eocene and Oligocene times this land foundered and the present mountain chains came into being. During the Oligocene, Tobago probably formed part of the continent but was separated by submergences during the Miocene. There is evidence of a Miocene shore-line at the southwestern end of the island. In Pliocene times it is probable that Tobago was once more united with the mainland, only to become detached again soon afterwards. Tobago has now probably led a separate existence for at least 500,000 years.

SOILS

Certain agricultural soils of Tobago were described by Hardy, Akhurst, and Griffith (1931), who distinguished four main soil-types for the cacao districts: residual soils derived from basic igneous rocks, residual soils derived from metamorphic sedimentary rocks, alluvial soils derived from igneous rocks, and alluvial soils derived from metamorphic sediments. All the soils examined appeared remarkably similar, being immature and without profound leaching

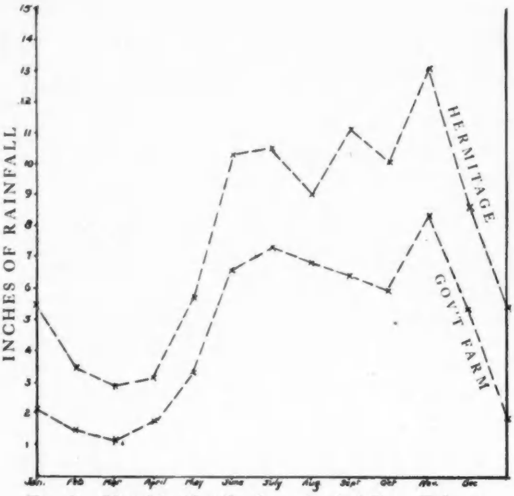

FIG. 3. Monthly distribution of rainfall on Tobago.

FIG. 4. Mangroves.

FIG. 5. Typical vegetation on Little Tobago—deciduous seasonal forest. A large leafless *Lonchocarpus domingensis* at right, abundant Coccothrinax palms in center, while the large leaves of *Anthurium Hookeri* show near the ground.

FIG. 6. Little Tobago; cliff vegetation of the windward shore. Windswept thicket at top containing *Cephalocereus moritzianus;* lower, turf of recumbent succulent herbs with *Cactus Broadwayi.*

effects; they were relatively shallow soils, seldom exceeding 36 inches in depth, light in texture, neutral in reaction and containing appreciable amounts of organic matter. A single profile was examined in a forest area, at King's Bay Estate, altitude 950 feet, over igneous rock. This soil was bright red throughout its whole depth and was highly leached and acidic in reaction. Parent rock had not appeared at 72 inches in depth.

Sporadic auger-borings were made by the writer on enumeration traverses in the Forest Reserve, from which two main soil-types could be distinguished generally corresponding to Hardy's "Residual soils derived from basic igneous rock" and "Residual soils derived from metamorphic sedimentary rocks." Owing to the nature of the country it is doubtful if the Reserve contains any alluvial soil. No red soil in any way resembling Hardy's King's Bay Estate profile was encountered at any time: igneous soils were found to be invariably speckled brown-green in color. A typical profile was selected, sampled, and described for each of the two soil types. Descriptions of the profiles are given in Tables 2 and 3. Samples were taken from the profiles at various depths and brought to Trinidad, where in kindness to the writer they were analysed by Professor F. Hardy at the Imperial College of Tropical Agriculture. The results of the laboratory analysis, together with Professor Hardy's comments, are given in Table 4. The same table contains also for comparative purposes data kindly furnished by Professor Hardy from partial analyses of two other forest soil profiles on igneous rock; the first set (T. B. 364-367) was collected by G. Milne and E. M. Chenery in March, 1938 at the 3½ M.P. on the Easterfield-Mason Hall Road in second growth forest not far from the Reserve, and the other (T. B. 368) was collected by F. Hardy in March, 1940 at the 6½ M.P. on the St. George-Castara Road in forest quite near the writer's profile No. 1. These soils are both much less acid than the writer's, but the surface samples agree in the small amount of available phosphate and the single potash value is very low. Deficiency of available phosphate and potash seems to be characteristic of these soils.

The most important features of these soils from the point of view of the forest vegetation are as follows:

No. 1 is a free-draining sandy soil where water percolates rapidly—shown by the deep penetration of organic matter and the absence of red mottling. Auger borings usually showed this soil to be quite dry at 24 inches in depth, though the surface was moist. It appears that the underlying igneous rock has been so shattered by dynamo-metamorphism that it permits very free downward percolation of soil water; this water does not lie for a sufficiently long time in contact with the surface of the rock to effect any intense hydrolysis, and red "lateritic" decomposition products do not occur. This is a shallow soil, rotten rock being encountered at only 18 inches depth, below which very few roots appeared to penetrate.

No. 2 is a heavy clay soil with impeded internal drainage, shown by the low penetration of organic matter and the appearance of crimson mottling at the base of the profile. There is probably little internal water movement. This is a deep soil into which roots penetrate to a considerable depth.

According to Charter's hypothesis (1941) the character of the profile shows it to have reached at least the initial stage in the maturity sequence for such a soil derived from sedimentary deposits.

LAND USAGE AND SETTLEMENT

In pre-Columbian times Tobago was inhabited by Caribs, a coastal people who practised a small amount of shifting cultivation but relied mainly on hunting and collecting. The island was discovered for the western world by Columbus in 1498 but no European settlement took place until 1632. Much internecine fighting followed between English, French, and Dutch, the island changing hands many times until the close of the Napoleonic Wars. Since 1814 the island has been continuously under the British Crown, first enjoying separate government; declining prosperity led later to the union of Tobago politically with Trinidad.

The census of 1931 showed the population to be 25,358, a density of 222 to the square mile. The present-day population is almost wholly of African descent and composed largely of peasants.

In the old, unsettled days before 1814 Tobago was one of the most valuable pieces of territory in the world, because of the great wealth of sugar produced there. This was virtually the sole crop and was cultivated on all the available accessible land in the island in spite of the mountainous nature of the country. Old maps exist showing the boundaries of the sugar estates and listing the number of slaves kept on each. From these maps it appears that the areas which are now the Crown Lands and Forest Reserve were never cultivated, being too inaccessible, except possibly the top of Pigeon Hill, which has been in private hands. For many years the former importance of sugar continued. A government map of 1840 shows the boundaries of the old estates, a good many new blocks surveyed out in the interior on the Crown Lands as though these were being offered for sale and a "Rain Reserve" or strip of Crown Land to be retained as forest along the crest of the Main Ridge. Subsequently, however, sugar began to decline and it appears that no further Crown Lands were taken up. The nature of the island rendering rationalization of the industry impracticable, sugar cultivation has gradually disappeared from Tobago. The estates went over one by one to secondary bush and shifting cultivation by peasants. In the last 40 years cacao has been introduced to a large extent in the moister parts of the island.

TABLE 1. Rainfall of Tobago.

Stations and No. Years of Records		Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sep.	Oct.	Nov.	Dec.	Total
Botanic Station (31 years)	Average Ave. no. days	3.59 16	2.24 12	1.66 10	2.42 12	4.70 15	9.02 23	9.25 23	7.99 20	7.76 19	7.76 18	9.89 22	6.52 20	72.80 210
Charlotteville Estate (11 years)	Average Ave. no. days	5.97 15	2.92 10	2.01 9	3.70 9	5.12 11	8.37 14	8.23 17	8.46 15	8.90 15	8.81 17	14.73 19	9.34 15	86.56 166
Government Farm (31 years)	Average Ave. no. days	2.07 7	1.46 6	1.15 5	1.73 6	3.30 10	6.53 15	7.26 16	6.78 14	6.44 13	5.87 12	8.32 15	5.28 13	56.19 132
King's Bay (31 years)	Average Ave. no. days	4.89 13	3.63 11	2.61 10	3.01 11	5.04 13	8.91 19	9.11 21	7.69 18	9.38 17	8.31 17	11.01 20	7.65 18	81.24 188
Hermitage Estate (31 years)	Average Ave. no. days	5.40 9	3.42 6	2.84 6	3.14 6	5.70 9	10.27 15	10.49 16	9.00 14	11.12 11	10.02 15	13.08 15	8.60 14	93.08 136
Kendal Estate (19 years)	Average Ave. no. days	5.36 24	3.59 19	2.56 17	3.45 16	5.10 19	9.81 25	9.34 26	9.47 24	9.90 22	9.22 24	14.48 27	10.18 26	92.46 269

Stations	Driest Month			Wettest Month			Driest Year			Wettest Year		
	Month and Year	Ins.	Days	Month and Year	Ins.	Days	Year	Ins.	Days	Year	Ins.	Days
Botanic Station	3/1934	0.11	3	11/1933	20.99	28	1914	51.74	–	1938	100.84	207
Charlotteville	5/1941 3/1924	0.0	–	11/1938	32.97	27	1934	66.03	112	1938	137.03	187
Government Farm	5/1930 3/1914	0.0	–	11/1938	24.10	22	1914	31.42	–	1938	130.64	154
King's Bay	3/1934	0.14	5	11/1938	24.61	27	1914	56.10	–	1933	120.19	215
Hermitage Estate	3/1934	0.0	–	11/1938	27.48	24	1914	68.62	–	1938	132.56	170
Kendal Estate	3/1924	0.0	–	11/1938	33.28	30	1930	63.67	–	1938	169.76	293

TABLE 2. Soil Profile No. 1 on St. George-Castara Road between 6¼ and 6½ M.P. in forest of the Gooseberry-Blue Copper type.

DRAINAGE: PROFILE—
Internally: Very free
Externally: Free
Site: Permanently moist

Parent material: Basic igneous rocks (epidiorite)
Topography: Mountain side
Aspect: East

Horizons	Color	Texture	Mineral Skeleton	Structure	Porosity	Consistency	Roots	Water condition
Surface	Very thick mat of humus and nutty soil containing most of roots							
0″ - 12″	Dark brown, slightly speckled, greenish-white	Clay-silt	Stoneless	Nutty	Spongy	Loose	Few, all sizes	Just moist
12″ - 18″	Brown, speckled greenish-white	Light loam	ditto	Crumb	Fissured	Compact	ditto	ditto
18″ - 66″	Olive-brown speckled yellow-brown	Parent rock, decomposed but retaining its structure	Parent rock, decomposed but hard	Structure of rock retained	ditto	Indurated	Very few	ditto
Below 66″	Olive-green speckled brown, white and green							

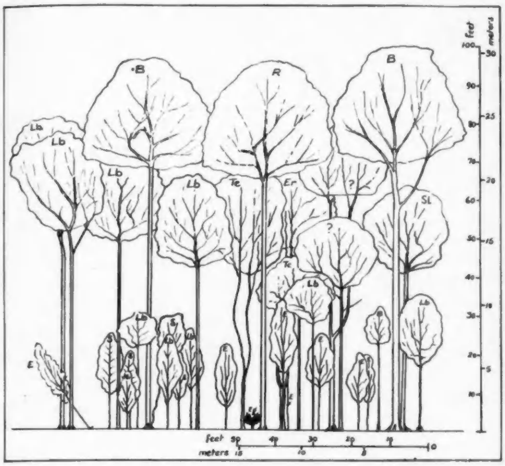

FIG. 7. Profile diagram of Lower Montane Rain Forest measured in the reserve near the Parlatuvier Road.

FIG. 8. Undergrowth in Lower Montane Rain Forest. The small buttresses are typical of the dominants in this type. The tree is *Erythroxylum impressum.*

FIG. 9. Lower Montane Rain Forest.
Note: (i) General impression of luxuriant forest.
(ii) Tall straight stems of the trees.
The large trees are *Sloanea trinitensis* and *Erythroxylum impressum.*

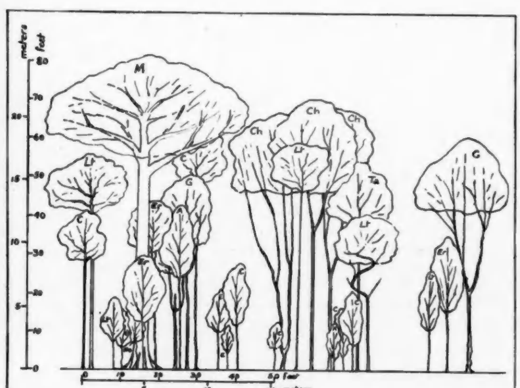

FIG. 10. Profile diagram of Xerophytic Rain Forest, measured in the reserve near the St. George-Castara Road.

TABLE 3. Soil Profile No. 2 on Roxborough-Parlatuvier Road between 4½-4¾ M.P. in forest of the Rosewood-Redwood type.

DRAINAGE: PROFILE—
Internally: Somewhat impeded
Externally: Free

Site: Permanently moist

Parent material: Schist
Topography: Mountain side
Aspect: West

Horizons	Color	Texture	Mineral Skeleton	Structure	Porosity	Consistency	Roots	Water condition
Surface 0″ - 9″	Good humus mat Yellow	Clay	Stoneless	Cloddy	Fissured	Tenacious	Many, all sizes	Wet
9″ - 30″	Yellow-orange	Silty clay	ditto	ditto	ditto	ditto	ditto	ditto
30″ - 50″	Orange, mottled crimson	Silty clay	ditto	Shows original structure	ditto	ditto	ditto	ditto
Below 50″	Predominently orange, mottled crimson, black and white	Silty weathered parent material	Parent rock, decomposed and soft but retaining its structure					

TABLE 4. Results of laboratory analysis of profile samples submitted by Mr. J. Beard, Asst. Conservator of Forests, March, 1942.
PROFILE No. 1: developed over *diorite*.
PROFILE No. 2: developed over *quartz-mica-schist*.

Soil No.		Depth (ins.)	M.P.S. %	Sand %	I.T.	Norm. pH	REACTION Exch. pH	O.M. %	Avail. P_2O_5 (p. p. m.)	Avail. K_2O
	PROFILE No. 1: *St. George – Castara Road. (Gooseberry – Blue Copper Association)*									
TB. 370	Mat; crumb	Surface	–	–	–	4.3	3.9	–	–	–
371	Brown	12	27.8	38.4	20	6.5	5.5	1.79	3	43
372	Speckled	18	41.2	60.7	29	6.4	5.4	2.70	3	–
373	Rotten rock (Igneous)	66	Sandy	83.4	–	7.1	5.7	0.70	4	–
	PROFILE No. 2: *Roxborough – Parlatuvier Road. (Rosewood-Redwood Association)*									
374	Mat; crumb	Surface	–	–	–	4.1	3.6	–	–	–
375	Yellow	9	69.3	9.9	67	4.5	3.8	4.23	3	53
376	Orange	30	53.8	19.5	50	4.6	3.8	1.46	3	–
377	Red mottled	50	49.1	20.2	45	4.6	3.9	1.57	3	–
378	Rotten rock (Schist)	Below 50	42.7	34.0	36	4.7	4.0	0.39	5	–

COMPARATIVE DATA:

Soil No.		Depth (ins.)	Coarse and fine sand %	I.T.	pH	O.M. %	Total N %	Avail. P_2O_5 (p.p.m.)	Avail. K_2O
TB. 367	Brown soil	12	16	–	6.1	–	–	6	–
365	Whitish clay	24	47	–	6.8	–	–	8	–
366	ditto	36	51	–	7.1	–	–	135	–
364	Rotten rock	54	74	–	6.4	–	–	240	–
368	Rotten rock	24–36	44	26	6.9	0.5	0.04	11	4.3

REMARKS.

PROFILE No. 1: This seems a typical diorite profile (see "Soils of Tobago"). It is a slightly acid loam, containing a medium-low content of organic matter which appears to penetrate deeply. The contents of available phosphates and of available potash are very low for an agricultural soil. The actual samples perhaps represent an infertile phase of this soil-type.

PROFILE No. 2: This is a heavy clay soil, and shows a marked physical contrast to No. 1. It is very highly acid at all depths; its contents of organic matter is medium-high in the surface 9 ins. layer, diminishing downwards, and insignificant below the 50-inch depth. As in No. 1 the contents of available phosphates and available potash are extremely low (for an agricultural soil), and the samples might be regarded as representing an infertile phase. The main differences between the two profiles are (a) the very high acidity of No. 2, (b) the sandy texture of No. 1 as compared with the clayey texture of No. 2. (Signed) F. HARDY.

In 1904 and subsequently, areas now totaling 9,776 acres comprising the old Rain Reserve and adjacent Crown Lands on the Main Ridge were proclaimed as Forest Reserve in perpetuity for the purpose of maintaining protective forest cover on the watersheds. The remaining Crown Lands (4,514 acres in 1938) are available for sale but there is very little pressure on the land and hardly any is ever applied for. The Forest Reserve and Crown Lands excepting Pigeon Hill represent, therefore, areas of forest which is probably almost all primeval, none of the land having been under either continuous or shifting cultivation. Forest fires appear to be unknown, so that the only human interference is in the form of sporadic felling of trees for timber. The forests are so inaccessible, however, that the effect of this is negligible, the average annual cut for the last 8 years, for example, having been only 150 trees from the Crown Lands, or 1 per 30 acres of forest, and 195 trees from the Reserve, or 1 per 50 acres.

The island of Little Tobago (280 acres) which is now Crown property was formely in private hands and much of it was cultivated for sea-island cotton. Early in the present century the owner—Sir William Ingram—discontinued cultivation and allowed the island to revert to bush. He made it a bird sanctuary and imported birds of paradise from New Guinea; on his death the island was presented to the government on condition that it be maintained as a Game Reserve. The island's vegetation today is homogenous and it is not possible to tell what parts were formerly under cultivation. No timber exploitation takes place there.

THE FLORA

The flora of Tobago is entirely continental in its affinities. Belonging structurally to the South American mainland and not to the Lesser Antilles, Tobago is no oceanic island, but received its flora during Eocene or Oligocene times when actually forming a part of the continent. For this reason the flora corresponds in a close degree with that of Trinidad. It is by no means as rich, due to the disparity in size of the two islands. Trinidad, twelve times as large, contains many plants of swamps, savannas, and high mountain woodland—among other formations—assemblages which are not found in Tobago. Table 8 gives a provisional list of trees native to Tobago, compiled from the published parts of the Flora of Trinidad and Tobago and from the Trinidad Herbarium in Port of Spain. The list contains 162 species in 121 genera and 50 families. The following trees appear to be endemic to Tobago:

Psychotria tobagensis Urb. A common understory tree in rain forest, almost a shrub.
Tresanthera pauciflora K. Schum. A most extraordinary plant: a large shrub with large leaves and long rambling branches sometimes almost recumbent. Abundant in rain forest understory.
Sloanea sp. (undescribed). A large tree very similar to *Sloanea trinitensis*, but differing mainly in that the fruit is white inside and not crimson.
Euterpe sp. (undescribed). "Mountain cabbage." Broadway (1916) lists this palm as *Euterpe globosa* Gaertn., almost certainly wrongly.
Bactris Sworderiana Becc. Doubtful. May be synonymous with *Bactris Cuesa* Crueg. of Trinidad.
Duguetia tobagensis Urb.
Myrcia tobagensis Urb.
Guettarda tobagensis Urb.

It is interesting to note that one of the commonest forest trees, *Ternstroemia oligostemon* Kr. & Urb. is an Antillean which is not found in Trinidad.

FIG. 11. Xerophytic Rain Forest.
Note: (i) General impression of a small pole forest.
(ii) Bark-peeling trees in the foreground—left, *Guettarda scabra;* right, *Amomis caryophyllata.*

Another such species is *Lonchocarpus domingensis* (Pers.) DC., but apart from a few coastal shrubs, this is the sum total of strictly Antillean affinity in the flora. Conversely, several species belonging to the mainland occur abundantly in Tobago but in Trinidad are absent or exceedingly rare. Among these are:

Amomis caryophyllata (Jacq.) Kr. & Urb.
Conomorpha peruviana DC.
Chione venosa (Sw.) Urban
Eschweilera decolorans Sandwith
Simaruba amara Aubl.
Guettarda scabra Lam.

This may appear somewhat peculiar. Amomis, Guettarda, and Chione belong to the formation xerophytic rain forest which is not represented in Trinidad. The identification of the tree "devilwood" as *Eschweilera decolorans* Sandwith is uncertain and the tree may prove to be a Tobago endemic. The case of Simaruba is a strange one. Similarly several species abundant in the Northern Range of Trinidad are almost absent from Tobago.

The local names of trees in Tobago are "Creole" names, those used by the aboriginal Caribs having

TABLE 5. Carapa-Andira Association (Crabwood-Angelin Forest). Average composition per 10 acres, as shown by enumeration.

Creole Name	Botanical Name	Abundance	Constancy	Exclusiveness	Number in Girth Classes					
					6 - 7 ft.	7 - 8 ft.	8 - 9 ft.	9 - 10 ft.	Over 10 ft.	Total
1. UPPER STORY:										
1. Crabwood	*Carapa guianensis* Aubl.	v.a.	5	con.	22	4	10	2	10	48
2. Angelin	*Andira inermis* H. B. K.	a.	5	a.c.	18	4	8			30
3. Horseflesh	*Hieronyma caribaea* Urb.	a.	4	a.c.	12		6		6	24
4. Devilwood	*Eschweilera decolorans* Sandwith.	a.	5	ind.	12	4	4			20
5. Wild nutmeg	*Virola surinamensis* (Rol.) Warb.	f.	5	con.	6	2	4		2	14
6. Soapwood	*Pithecellobium jupunba* (Willd.) Urb.	f.	3	ind.	10		2		2	14
7. Duckwood	*Ocotea leucoxylon* (Sw.) Mez.	f.	5	ind.	8		2	2		12
8. Greenheart	*Tabebuia serratifolia* (Vahl.) Nichols.	o.	2	ind.	6					6
9. Redwood	*Ternstroemia oligostemon* Kr. & Urb.	o.	2	cas.	4					4
10. Lionwood	*Sloanea trinitensis* Sandwith.	o.	1	cas.	2		2			4
11. Timber Fiddlewood	*Vitex divaricata* Sw.	o.	2	ind.	2		2			4
12. Silk cotton	*Ceiba pentandra* (L.) Gaertn.	o.	2	ind.					4	4
13. Galba	*Calophyllum ludidum* Benth.	o.	2	cas.	4					4
14.	*Licania ternatensis* Hook f.	o.	3	cas.	4					4
15.	*Micropholis Cruegeriana* Pierre	o.	1	cas.		2	2			4
16. Bitter Quassia	*Simaruba amara* Aubl.	r.	3	cas.			2			2
17. Rosewood	*Byrsonima spicata* Rich.	r.	2	cas.	2					2
18. Hogplum	*Spondias mombin* L.	r.	1	ind.	2					2
19. Goatmeat	?	r.	2	ind.	2					2
20. Yellow sanders	*Buchenavia capitata* (Vahl.) Eichl.	r.	1	ind.			2			2
21. Beefwood	*Pisonia* sp.	r.	1	ind.	2					2
22.	*Matayba arborescens* Radlk.	r.	2	ind.			2			2
23. Unknown		r.			2					2
					120	16	48	4	24	212

Creole Name	Botanical Name	Abundance	Constancy	Exclusiveness	Number in Girth Classes					
					2 - 3 ft.	3 - 4 ft.	4 - 5 ft.	5 - 6 ft.		Total
2. MIDDLE STORY:										
1. Mountain Cabbage	*Euterpe* sp.	v.a.	5	ind.	220					220
2. Devilwood	*Eschweilera decolorans* Sandwith	a.	5	ind.		32	14	12		58
3. Angelin	*Andira inermis* H. B. K.	a.	5	a.c.		10	18	6		34
4. Wild cocoa (A)	*Licania biglandulosa* Griseb.	a.	5	ind.		18	8	2		28
5. Crabwood	*Carapa guianensis* Aubl.	a.	5	con.		8	16	4		28
6. Duckwood	*Ocotea leucoxylon* (Sw.) Mez.	a.	5	ind.		14	10	2		26
7. Wild nutmeg	*Virola surinamensis* (Rol.) Warb.	a.	5	con.		6	14	4		24
8. Wild cocoa (B)	*Marila grandiflora* Griseb.	l.a.	3	ind.		18	4	2		24
9. Myers	*Lauraceae* spp.	a.	5	ind.		16	4	2		22
10. Soapwood	*Pithecellobium jupunba* (Willd.) Urb.	f.	3	a.c.		4	4	4		12
11. Small-leaf	*Myrtaceae* spp.	f.	5	ind.		6	4			10
12. Horseflesh	*Hieronyma caribaea* Urb.	f.	4	a.c.			4	4		8
13. Bitter Quassia	*Simaruba amara* Aubl.	f.	3	cas.		2	6			8
14. Greenheart	*Tabebuia serratifolia* (Vahl.) Nichols.	f.	2	ind.		2	6			8
15. Timber Fiddlewood	*Vitex divaricata* Sw.	o.	2	ind.		4	2			6
16.	*Licania ternatensis* Hook f.	o.	3	cas.		2	4			6
17. Redwood	*Ternstroemia oligostemon* Kr.	o.	2	cas.			2	2		4
18.	*Alchornea glandulosa* Poepp.	o.	1	ind.			2	2		4
19. Rough palm	*Scheelea osmantha* Barb.	o.	1	con.	4					4
20.	*Matayba arborescens* Radlk.	o.	2	ind.		2	2			4
21. Bois flot	*Ochroma pyramidale* (Cav.) Urb.	o.	1	ind.		2	2			4
22. Wild manjack	*Cordia* spp.	o.	2	ind.		2		2		4
23. Pois doux	*Inga punctata* Willd.	o.	1	con.		4				4
24. Rosewood	*Byrsonima spicata* Rich.	r.	2	cas.				2		2
25. Lionwood	*Sloanea trinitensis* Sandwith.	r.	1	cas.				2		2
26. Goatmeat	?	r.	2	ind.		2				2
27.	*Erythroxylum impressum* O. E. Schulz.	r.	1	cas.		2				2
28. Cabbage palm	*Roystonea oleracea* Cook	r.	2	con.		2				2
29. Beefwood	*Pisonia* sp.	r.	1	ind.				2		2
30. Unknown	?	r.					2			2
					224	158	128	54	....	564

TABLE 5 *(Continued)*

Creole Name	Botanical Name	Abundance	Constancy	Exclusiveness	Number in Girth Classes 1 - 2 ft.	2 - 3 ft.	3 - 4 ft.			Total
3. LOWER STORY:										
1. Mountain Cabbage	*Euterpe* sp.	v.a.	5	ind.	278					278
2. Small-leaf	*Myrtaceae* spp.	a.	5	ind.	42	52				94
3. Wild cocoa (A.)	*Licania biglandulosa* Griseb.	a.	5	ind.	44	28				72
4. Wild Waterwood	*Tresanthera pauciflora* K. Schum.	a.	4	a.c.	32	16				48
5. Crabwood	*Carapa guianensis* Aubl.	a.	5	con.	28	14				42
6. Duckwood	*Ocotea leucoxylon* (Sw.) Mez.	a.	5	ind.	16	26				42
7. Wild coffee	*Styrax glaber* Sw.	a.	4	ind.	30	8	2			40
8.	*Rudgea Freemani* Sprague & Williams	f.	4	ind.	18	16	2			36
9. Wild cocoa (B.)	*Marila grandiflora* Griseb.	f.	3	ind.	16	18				34
10. Devilwood	*Eschweilera decolorans* Sandwith.	f.	5	ind.	10	18				28
11. Myers	*Lauraceae* spp.	f.	5	ind.	6	20				26
12.	*Stylogyne lateriflora* (Sw.) Mez.	f.	3	a.c.	12	10	2			24
13. Trumpet	*Cecropia peltata* L.	o.	1	ind.	4	8				12
14. Wild nutmeg	*Virola surinamensis* (Rol.) Warb.	o.	5	con.	4	6				10
15.	*Matayba arborescens* Radlk.	o.	2	ind.	2	6				8
16. Parrot apple	*Clusia rosea* Jacq.	o.	1	cas.		8				8
17. Bitter Quassia	*Simaruba amara* Aubl.	o.	3	cas.	4	2				6
18. Yellow Wattle	*Vismia falcata* Rusby	o.	1	ind.	2	4				6
19. Angelin	*Andira inermis* H. B. K.	o.	5	a.c.	4					4
20. Soapwood	*Pithecellobium jupunba* (Willd.) Urb.	o.	3	a.c.	2	2				4
21.	*Licania ternatensis* Hook f.	o.	3	cas.		4				4
22. Galba	*Calophyllum lucidum* Benth.	r.	2	cas.		2				2
23. Wild manjack	*Cordia* spp.	r.	2	ind.		2				2
24. Burn-nose	?*Anaxagorea acuminata* St. Hil.	r.	1	ind.	1	1				2
25. Unknown		r.			2					2
					557	271	6			834
	Total all individuals									1,610

disappeared. Since Tobago has never been an island in which Creole-French was spoken, the "Creole-English" West Indian tree vocabulary is in use. Names therefore differ from those now in common use in Trinidad and Grenada but agree to a considerable extent with those current in St. Vincent. This English vocabulary is very poor compared with the Creole-French. Plants of the coast and cultivated lands are well known and recognized, but up on the Main Ridge only the most conspicuous trees or those which are worked for their timber are dignified with local names. The remainder are classed vaguely as "wild trees." In Trinidad almost every tree is named. Of the 84 tree species the writer recorded on enumeration traverses on the Main Ridge, local names were obtained for 60, the remaining 24 apparently not being distinguished. Local nomenclature agrees with common West Indian practice in using group terms for certain closely allied or similar groups of plants. Thus:

''Myers'' for Lauraceae (Trinidad and Grenada ''laurier,'' St. Vincent ''sweetwood'').

''Small-leaf'' for Myrtaceae (Trinidad ''wild guava,'' Grenada ''guyavier,'' St. Vincent ''bashie guava'').

''Wild spice'' for Melastomaceae (Trinidad ''sardine,'' Grenada ''bois cendre,'' St. Vincent ''ashes wood'').

''Wild manjack'' for *Cordia* spp. (Trinidad ''lay-lay'' or ''manjack,'' Grenada and St. Vincent ''manjack'').

Secondary differentiation of the group term such as occurs in Creole-French (laurier canelle, laurier 'zaboca, laurier mama 'zenfants) is not, however, practiced in Tobago, in common with the general poverty of names.

In the lists of species names appearing in inverted commas are those invented for convenience by the writer.

In the lists of species for the various associations (Tables 5, 6, and 7), an endeavor has been made to indicate degree of abundance, constancy, and exclusiveness, the following symbols being used:

Abundance: in 5 degrees—v.a. = very abundant, a = abundant, f = frequent, o = occasional, r = rare.

Constancy: in 5 degrees—5 = occurs in over 80 percent of the areas enumerated, 4 = occurs in 60 to 80 percent, 3 = in 40 to 60 percent, 2 = in 20 to 40 percent, 1 = in below 20 percent.

Exclusiveness: in 4 degrees—con. = confined to the association, characteristic of it and occurring only casually elsewhere; a.c. = almost confined, occurring more commonly in the association than elsewhere; ind. = indifferent, occurring as readily elsewhere; and cas. = casual, an intruder characteristic of some other type.

THE PLANT COMMUNITIES

The Formations

The plant formations found on this island are an expression of the interplay of the environmental factors of climate, topography, and soil. They will be arranged into four groups—the mangrove woodland, the littoral woodland, the seasonal forests, and the rain forests—following, with some slight modifications made for greater convenience in this particular study, the system of nomenclature and classification advocated by Beard (1942, 1944).

Mangrove woodland. Mangrove is found on tidal mudflats or shallow lagoons where fresh and salt water mingle. There is no need to detail the well-known specializations of mangrove species.

Littoral woodland is found fringing the sea coasts, on beaches, sandbanks, and cliffs, where salt spray is frequently deposited on the vegetation. Many plants composing this formation are adapted to withstand the effects of a salt coating on their leaves, which are thick and fleshy and have a waxy covering.

Seasonal forests. In the small, climatically oceanic and mountainous islands of the Caribbean the vegetation between the coast and a point varying between some 400 and 1,200 feet elevation in the mountains is primarily influenced by the rainfall regime. Coastal areas are always dry, with an annual precipitation as low as 40 inches in places and a most severe season of drought during a part of the year. The available moisture, however, steadily increases from the coast toward the central mountains until a point is reached on the lower slopes where a dry season to all intents and purposes has ceased to exist. The seasonal forests vary from low to tall and from deciduous to evergreen and represent the decreasing influence of drought between the arid coast and the rain forest zone. In Tobago nearly all seasonal vegetation has been destroyed by the cultivator.

Rain forests. In the mountainous interior rainfall still fluctuates seasonally but is adequate to sustain growth during the dry season months. Rain forest, the optimum tropical vegetation, is found here, and covers the whole of the Main Ridge. The summits in Tobago do not ascend sufficiently high for any very adverse effects of exposure and lowered temperature to be felt, so that the more specialized montane formations do not appear. Local variations in the

Table 6. Byrsonima-Licania Association. Ternstroemia Faciation (Rosewood-Redwood Forests). Average composition per 10 acres, as shown by enumeration.

Creole Name	Botonical Name	Abundance	Constancy	Exclusiveness	Number in Girth Classes							
					4 - 5 ft.	5 - 6 ft.	6 - 7 ft.	7 - 8 ft.	8 - 9 ft.	9 - 10 ft.	Over 10 ft.	Total
1. Upper Story:												
1. Rosewood	*Byrsonima spicata* Rich.	v.a.	5	a.c.	15	7	16	4	2	....	1	45
2. Wild cocoa	*Licania biglandulosa* Griseb.	a.	5	ind.	22	3	5	....	1	....	....	31
3. Redwood	*Ternstroemia oligostemon* Kr. & Urb.	a.	5	a.c.	14	5	8	1	1	....	....	29
4. Devilwood	*Eschweilera decolorans* Sandwith	a.	5	ind.	12	4	8	1	2	....	1	28
5. "Red" Lionwood	*Sloanea trinitensis* Sandwith	a.	4	a.c.	3	5	5	3	6	2	1	25
6. Bitter Quassia	*Simaruba amara* Aubl.	f.	5	a.c.	7	5	4	1	1	....	....	18
7. Duckwood	*Ocotea leucoxylon* (Sw.) Mez	f.	4	ind.	6	1	2	....	1	....	....	10
8. Soapwood	*Pithecellobium jupunba* (Willd.) Urb.	f.	3	ind.	2	1	2	1	4	....	....	10
9.	*Erythroxylum impressum* O.E. Schulz.	f.	4	ind.	5	2	2	....	....	....	....	9
10. Angelin	*Andira inermis* H. B. K.	f.	3	cas.	3	1	1	1	1	1	1	9
11. "White" Lionwood	*Sloanea* sp.	f.	2	a.c.	2	1	2	1	1	....	1	8
12. Horseflesh	*Hieronyma caribaea* Urb.	o.	4	cas.	1	1	2	1	1	1	....	7
13.	*Richeria grandis* Vahl.	l.f.	2	con.	3	1	2	....	....	....	....	6
14. Myers	*Lauraceae* sp.	o.	4	ind.	3	1	2	....	....	....	....	6
15.	*Matayba arborescens* Radlk.	o.	3	ind.	2	1	1	....	....	....	....	4
16. Galba	*Calophyllum lucidum* Benth.	o.	2	cas.	....	....	1	1	1	1	....	4
17. Goatmeat	?	r.	2	ind.	1	....	1	....	1	....	....	3
18. Yellow Sanders	*Buchenavia capitata* (Vahl.) Eichl.	r.	1	ind.	....	1	....	1	....	1	....	3
19. Crabwood	*Carapa guianensis* Aubl.	r.	1	cas.	1	1	1	....	....	....	....	3
20. Wild nutmeg	*Virola surinamensis* (Rol.) Warb.	r.	1	cas.	1	1	1	....	....	....	....	3
21.	*Roupala montana* Aubl.	r.	1	ind.	1	2	....	....	....	....	....	3
22. "Redbark"	?	r.	1	con.	1	....	1	....	....	....	....	2
23. Bowldish	*Ficus* sp.	r.	2	ind.	....	1	1	....	....	....	....	2
24. Timber Fiddle-wood	*Vitex divaricata* Sw.	r.	1	ind.	1	....	....	....	1	....	....	2
25. "Warty-bark"	?	r.	2	con.	1	....	....	....	....	....	....	1
26. Cabbage palm	*Roystonea oleracea* Cook	r.	1	cas.	1	....	....	....	....	....	....	1
27. "Red Polish"	?	r.	1	con.	....	....	....	1	....	....	....	1
28. Tobago Yoke	*Sloanea Purdiaei* Griseb.	r.	1	con.	....	....	1	....	....	....	....	1
29.	*Sapotaceae* sp.	r.	1	con.	1	....	....	....	....	....	....	1
30.	*Alchornea glandulosa*	r.	1	ind.	....	....	....	....	1	....	....	1
					109	45	69	17	25	6	5	276

TABLE 6 *(Continued)*

Creole Name	Botonical Name	Abundance	Constancy	Exclusiveness	Number in Girth Classes 1 - 2 ft.	2 - 3 ft.	3 - 4 ft.	4 - 5 ft.				Total
2. LOWER STORY:												
1. Mountain Cabbage	*Euterpe* sp.	l.v.a	3	ind.	137	88	...	...	...	...	...	225
2. Wild cocoa (A)	*Licania biglandulosa* Griseb.	v.a.	5	ind.	57	69	52	...	...	...	...	178
3. Small-leaf	*Myrtaceae* spp.	a.	5	ind.	52	28	7	...	...	...	...	87
4. Mountain Cabbage	*Euterpe Broadwayana* Becc.	l.v.a	3	ind.	63	11	...	...	...	...	...	74
5. Wild coffee	*Sytrax glaber* Sw.	a.	5	ind.	44	17	2	...	...	...	...	63
6. Devilwood	*Eschweilera decolorans* Sandwith	a.	5	ind.	17	23	22	...	...	...	...	62
7. Myers	*Lauraceae* spp.	f.	4	ind.	15	15	7	...	...	...	...	37
8. Bitter Quassia	*Simaruba amara* Aubl.	f.	5	a.c.	9	13	9	...	...	...	...	31
9. Duckwood	*Ocotea leucoxylon* (Sw.) Mez.	f.	4	ind.	8	11	10	...	...	...	...	29
10.	*Erythroxylum impressum* O. E. Schulz.	f.	4	ind.	3	14	10	...	...	...	...	27
11. Redwood	*Ternstroemia oligostemon* Kr. & Urb.	f.	5	a.c.	2	10	15	...	...	...	...	27
12. Rosewood	*Byrsonima spicata* Rich.	f.	5	a.c.	3	4	7	...	...	...	...	14
13.	*Rudgea Freemani* Sprague & Williams	o.	3	ind.	6	4	1	...	...	...	...	11
14. Wild cocoa (B)	*Marila grandiflora* Griseb.	l.f.	2	ind.	3	2	3	1	...	...	...	9
15. Goatmeat	?	o.	2	ind.	2	3	3	...	...	...	...	8
16.	*Matayba arborescens* Radlk.	o.	3	ind.	2	4	2	...	...	...	...	8
17. "Red" Lionwood	*Sloanea trinitensis* Sandwith	o.	4	a.c.	1	1	4	...	...	...	...	6
18.	*Richeria grandis* Vahl.	l.f.	2	con.	2	1	3	...	...	...	...	6
19.	*Psychotria tobagensis* Urb.	o.	1	ind.	6	...	...	...	...	...	...	6
20. Wild manjack	*Cordia* spp.	o.	2	ind.	1	4	1	...	...	...	...	6
21. Yellow wattle	*Vismia falcata* Rusby	o.	2	ind.	2	2	1	1	...	...	...	6
22.	*Cassipourea latifolia* Alston	o.	2	cas.	2	1	1	...	...	...	...	4
23. Wild nutmeg	*Virola surinamensis* (Rol.) Warb.	o.	1	cas.	1	2	1	...	...	...	...	4
24. Parrot-Apple	*Clusia rosea* Jacq.	r.	1	cas.	...	3	...	...	...	...	...	3
25.	*Eugenia confusa* DC.	r.	1	cas.	1	1	...	1	...	...	...	3
26. Tobago beau	*Brownea latifolia* Jacq.	r.	2	ind.	3	...	...	...	...	...	...	3
27.	*Roupala montana* Aubl.	r.	2	cas.	2	1	...	...	...	...	...	3
28. "Warty-bark"	?	r.	2	con.	1	1	...	...	...	...	...	2
29. Galba	*Calophyllum lucidum* Benth.	r.	2	cas.	1	...	1	...	...	...	...	2
30. Timber Fiddle-wood	*Vitex divaricata* Sw.	r.	1	ind.	1	...	1	...	...	...	...	2
31. "Redbark"	?	r.	1	con.	...	...	2	...	...	...	...	2
32.	*Stylogyne lateriflora* (Sw.) Mez.	r.	1	cas.	1	1	...	...	...	...	...	2
33. Field No. 78	?	r.	1	cas.	1	1	...	...	...	...	...	2
34. Angelin	*Andira inermis* H. B. K.	r.	3	cas.	...	...	2	...	...	...	...	2
35. "White" Lion-wood	*Sloanea* sp.	r.	2	a.c.	...	1	1	...	...	...	...	2
36. Soapwood	*Pithecellobium jupunba* (Willd.) Urb.	r.	3	ind.	1	...	...	...	...	...	...	1
37. Bowldish	*Ficus* sp.	r.	2	ind.	...	...	1	...	...	...	...	1
38. Crabwood	*Carapa guianensis* Aubl.	r.	1	cas.	1	...	...	...	...	...	...	1
39. Greenheart	*Tabebuia serratifolia* (Vahl.) Nichols.	r.	1	cas.	...	...	1	...	...	...	...	1
40. W. Waterwood	*Tresanthera pauciflora* K. Schum.	r.	1	cas.	1	...	...	...	...	...	...	1
41. Horseflesh	*Hieronyma caribaea* Urb.	r.	4	cas.	...	...	1	...	...	...	...	1
42. "Red Polish"	?	r.	1	con.	...	1	...	...	...	...	...	1
43.	*Alchornea glandulosa* Poepp.	r.	1	ind.	...	1	...	...	...	...	...	1
44. Beefwood	*Pisonia* sp. ?*eggersiana* Heimerl	r.	1	ind.	...	...	1	...	...	...	...	1
45. Yellow prickle	*Fagara* sp.	r.	1	cas.	1	...	...	...	...	...	...	1
46. Wild spice	*Miconia* sp.	r.	1	ind.	1	...	...	...	...	...	...	1
					454	338	172	3	...	...	...	967
	Total all individuals	...	...	...	...	...	...	...	...	...	...	1,243

environmental factors determine two sub-types of the main Rain Forest, which will be entitled respectively Lower Montane Rain Forest and Xerophytic Rain Forest.

THE ASSOCIATIONS

Since the flora of Tobago is basically identical with that of Trinidad it may be expected that the floristic groups or associations in the two islands will correspond in a like manner. Such occurs, however, only up to a point, beyond which the associations bear in many cases a curiously Antillean stamp. This is a fact which must presumably be explained on climatic grounds, since the climate of Tobago resembles that of the Lesser Antilles more closely than that of Trinidad.

Table 7. Manilkara-Guettarda Association (Gooseberry-Blue Copper Forest). Average composition per 10 acres, as shown by enumeration.

Creole Name	Botanical Name	Abundance	Constancy	Exclusiveness	Number in Girth Classes							
					4 - 5 ft.	5 - 6 ft.	6 - 7 ft.	7 - 8 ft.	8 - 9 ft.	9 - 10 ft.	Over 10 ft.	Total
1. Emergent trees:												
1. Gooseberry	*Manilkara bidentata* (A.DC.) Chev.	l.v.a	3	con.	20	2	7	....	7	1	4	41
2.	*Podocarpus coriaceus* Rich.	l.a.	3	con.	14	2	1	....	....	....	....	17
3. Parrot Apple	*Clusia rosea* Jacq.	f.	5	a.c.	7	1	....	....	....	....	....	8
4.	*Micropholis Cruegeriana* Pierre	f.	4	a.c.	5	3	....	....	....	....	....	8
5. Galba	*Calophyllum lucidum* Benth.	l.a.	2	a.c.	3	2	2	....	....	....	....	7
6.	*Licania ternatensis* Hook f.	l.f.	2	con.	4	....	....	....	....	....	....	4
7.	*Roupala montana* Aubl.	o.	5	a.c.	3	....	....	....	1	....	....	4
8. Bitter Quassia	*Simaruba amara* Aubl.	o.	2	cas.	4	....	....	....	....	....	....	4
9. Rosewood	*Byrsonima spicata* Rich.	r.	1	cas.	1	1	....	....	1	....	....	3
10. Lionwood	*Sloanea trinitensis* Sandwith	r.	1	cas.	....	....	1	....	....	....	....	1
11. Yellow Sanders	*Buchenavia capitata* (Vahl.) Eichl.	r.	1	ind.	....	....	....	....	1	....	....	1
					61	11	11	....	10	1	4	98
					1 - 2 ft.	2 - 3 ft.	3 - 4 ft.	4 - 5 ft.				Total
2. Trees forming the lower levels of the forest:												
1. Blue Copper	*Guettarda scabra* Lam.	l.v.a	3	con.	109	117	25	4	....	....	....	255
2. Small-leaf	*Myrtaceae* spp.	v.a.	5	ind.	155	50	9	....	....	....	....	214
3.	*Roupala montana* Aubl.	a.	5	a.c.	67	52	13	....	....	....	....	132
4. Parrot apple	*Clusia rosea* Jacq.	f.	5	a.c.	20	52	17	....	....	....	....	89
5.	*Cassipourea latifolia* Alston	f.	4	a.c.	63	23	1	....	....	....	....	87
6.	*Licania ternatensis* Hook f.	l.f.	2	con.	16	40	19	....	....	....	....	75
7. Bayleaf	*Amomis caryophyllata* (Jacq.) Kr.& Urb.	l.a.	3	con.	36	13	6	5	....	....	....	60
8. Mountain Cabbage	*Euterpe Broadwayana* Becc.	l.a.	2	ind.	51	9	....	....	....	....	....	60
9. Gooseberry	*Manilkara bidentata* (A.DC.) Chev.	l.a.	3	con.	12	20	27	....	....	....	....	59
10.	*Micropholis Cruegeriana* Pierre	l.f.	4	a.c.	19	31	8	....	....	....	....	58
11.	*Podocarpus coriaceus* Rich.	l.a.	3	con.	21	17	15	....	....	....	....	53
12.	*Erythroxylum impressum* O.E.Schulz	o.	2	ind.	29	4	4	1	....	....	....	38
13. "Pinkbark"	......?	l.f.	2	con.	15	15	5	....	....	....	....	35
14.	*Chione venosa* (Sw.) Urb.	l.f.	3	con.	8	11	4	....	....	....	....	23
15. Bitter Quassia	*Simaruba amara* Aubl.	l.o.	2	cas.	2	9	10	....	....	....	....	21
16. Wild cocoa	*Licania biglandulosa* Griseb.	o.	2	ind.	8	4	4	1	....	....	....	17
17. Mountain Cabbage	*Euterpe* sp.	l.f.	2	ind.	9	5	....	....	....	....	....	14
18. Redwood	*Ternstroemia oligostemon* Kr. & Urb.	r.	2	cas.	3	5	4	....	....	....	....	12
19. Galba	*Calophyllum lucidum* Benth.	r.	2	a.c.	2	2	1	....	....	....	....	5
20. Rosewood	*Byrsonima spicata* Rich.	r.	1	cas.	1	1	2	....	....	....	....	4
21. Greenheart	*Tabebuia serratifolia* (Vahl.) Nichols.	r.	1	cas.	2	2	....	....	....	....	....	4
22. Tobago beau	*Brownea latifolia* Jacq.	r.	2	ind.	4	....	....	....	....	....	....	4
23. Goatmeat	......?	r.	1	ind.	1	1	1	....	....	....	....	3
24. Wild spice	*Miconia* sp.	r.	1	ind.	2	....	....	....	....	....	....	2
25. Wild coffee	*Eugenia confusa* DC.	l.o.	2	a.c.	....	2	....	....	....	....	....	2
26. Beefwood	*Pisonia* sp. ?*eggersiana* Heimerl.	r.	1	ind.	1	1	....	....	....	....	....	2
27. Wild manjack	*Cordia* sp.	r.	1	ind.	1	1	....	....	....	....	....	2
28. Duckwood	*Ocotea leucoxylon* (Sw.) Mez.	r.	1	cas.	....	....	1	....	....	....	....	1
29. Trumpet	*Cecropia peltata* L.	r.	1	ind.	1	....	....	....	....	....	....	1
30. Wild milking	*Ficus* sp.	r.	1	ind.	1	....	....	....	....	....	....	1
31.	*Mouriri rhizophoraefolia* DC.	l.r.	1	con.	....	1	....	....	....	....	....	1
32.	*Psychotria tobagensis* Urb.	r.	1	ind.	1	....	....	....	....	....	....	1
33. Unknown	....	r.	....	.....	1	....	....	....	....	....	....	1
					661	487	176	11	....	....	....	1,335
	Total all individuals	....	....	....	....	....	....	....	....	....	....	1,433

The association of littoral woodland may be named from *Coccoloba uvifera* and *Hippomane mancinella*. This association is probably common to all the shores of the Caribbean. The mangrove (Rhizophora-Avicennia-Laguncularia) association has an even wider range and occupies the entire intertropical Atlantic seaboard of Africa and America. Deciduous seasonal forest is represented by the Bursera-Lonchocarpus association which is found, somewhat ruinate, in Trinidad and well developed throughout the Lesser Antilles. It is in the case of the rain forest associations that the convergence to Antillean pattern becomes noticeable. Xerophytic rain forest is not a formation which the writer has encountered elsewhere and its association, named from *Manilkara bidentata* and *Guettarda scabra*, is therefore at present unique but it contains several abundant species which while absent to very rare in Trinidad are common in the Lesser Antilles. The Carapa-Andira association of rain forest proper is not found in Trinidad, but we may conjecture from relics in Grenada and St. Vincent that it formerly occurred there. *Andira inermis* is a common tree in the islands but is rare in Trinidad and the mainland. The composition of lower montane rain forest is sufficiently homologous with that in the Northern Range of Trinidad to be considered as belonging to the same association, which may be named from *Byrsonima spicata* and *Licania biglandulosa*. The lower montane rain forest of Tobago is impressed with an Antillean physiognomy by several features, which may be purely coincidental but may equally be related to climate. First is the abundance (20 to 30 percent) in the lower story of a Euterpe palm, a feature of the Dacryodes-Sloanea association in the Windward Islands; large palms are virtually absent in the mountain forests of Trinidad. A second feature is the tendency to dominance of the genus Sloanea embracing several conspicuous trees with their large buttresses. All these Sloaneas are species endemic to Trinidad and Tobago and thus are not the same as those which are so prominent further north; but the effect is the same. As a third feature may be selected the abundance of *Ternstroemia oligostemon*, a tree of Antillean origin.

Trinidad possesses a very large number of species which are not found in Tobago; this may be largely ascribed to differences of habitat, for Trinidad contains numerous different types of vegetation, each with its characteristic species. The flora of freshwater swamp forest, of herbaceous swamp, palm swamp, marsh forests, woodland, and savannas is naturally not represented in Tobago, nor is that of montane rain forest and elfin woodland. Considering formations which exist in both islands, in the case of deciduous seasonal forest Tobago lacks notably *Machaerium robinifolium* (DC.) Vogel, *Capparis* spp., *Oliganthes condensata* Schulz., and *Lonchocarpus punctatus* H.B.K., the latter being replaced by *L. domingensis* (Pers.) DC. In the case of the rain forests, conspicuous absentees in Tobago are: *Sterculia caribaea* R. Br., *Terminalia obovata* (R. & P.) Steud., *Symphonia globulifera* L. Fil., *Tapirira guianensis* Aubl., *Lucuma Hartii* Hemsl., *Didymopanax morototoni* Dene & Planch., *Calliandra guildingii* Benth., and *Tabebuia stenocalyx* Sprague & Stapf. Further, a number of species abundant in the mountains of Trinidad are rare or localized in Tobago. *Licania ternatensis* Hook f., principal cropformer in lower montane rain forest in Trinidad is rare in the same formation in Tobago, being practically confined to xerophytic rain forest where it is frequent. *Chimarrhis cymosa* Jacq. is extremely rare in Tobago and though the writer collected the species it was not encountered on enumeration lines. *Manilkara bidentata* (A.DC.) Chev. is a most widespread tree in Trinidad occurring in almost every forest type; as an individual tree it reaches its finest development in rain forest, but it becomes gregarious in coastal woodland. In Tobago it is sharply confined to xerophytic rain forest. So also is *Podocarpus coriaceus* Rich. which is rare to occasional throughout evergreen types of forest in the north of Trinidad.

Conversely, several species common in Tobago become rare in Trinidad. *Simaruba amara* Aubl., *Matayba arborescens* Radlk., *Sloanea Purdiaei* Griseb., and *Ocotea leucoxylon* (Sw.) Mez. are examples in point.

DESCRIPTIONS OF COMMUNITIES

MANGROVE WOODLANDS

Nearly all the coastal swamps in Tobago have been drained or reclaimed and cultivated but certain relatively small areas remain where the necessary combination of tidal mudflats and brackish water permits the establishment of mangrove vegetation. The mangrove woodland of Tobago exhibits no unusual features. It corresponds with the general type so often and fully described already in the Caribbean and therefore merits no special treatment here. *Rhizophora mangle* L. is dominant nearest the open sea. Further into the swamp it is joined by *Avicennia nitida* Jacq. and *Laguncularia racemosa* (L.) Gaertn., while *Conocarpus erectus* L. is somewhat abundant at the landward fringes, occasionally with *Dodonaea viscosa* L. The fern *Acrostichum aureum* L. is virtually the only other component.

LITTORAL WOODLAND

The original sea-shore vegetation has persisted on cliffs, rocks, sandbanks, and small islets off the coast. Littoral woodland occurs frequently in localities where there is sufficient rainfall to promote a luxuriant growth, but structurally it exhibits always a dwarfed and windswept character—crowns distorted, branches gnarled, and pointing away from the wind—caused by the strong and constant sea-wind to which it is exposed and to the destructive effect of a coating of salt deposited on the leaves by spray. Some of the components are thorny, others laticiferous. The majority have fleshy and thickly cutinized leaves. According to exposure the stature of the woodland varies from shrubby to taller growth 20 or 30 feet

high. The component species of littoral woodland are frequently distributed by ocean currents. In Tobago as with mangrove, the littoral vegetation follows the general Caribbean pattern. The principal components of the Coccoloba-Hippomane association were noted as follows:

Coccoloba uvifera L.	Sea-grape
Hippomane mancinella L.	Manchineel
Citharexylum spinosum L.	Fiddlewood
Bursera simaruba (L.) Sarg.	Naked Boy
Pithecellobium unguis-cati (L.) Mart.	Black Jessie
Terminalia catappa L.	Almond
Chrysobalanus icaco L.	Fat pork
Pariti tiliaceum (L.) Juss.	Mahoe
Thespesia populnea (L.) Soland.	
Jacquinia barbasco (Loefl.) Mez.	Torchwood
Bourreria succulenta Jacq.	
Ficus Hartii Warb.	
Randia aculeata L.	
Bumelia buxifolia Willd.	
Trichilia trifolia L.	

SEASONAL FORESTS

Nearly all of the lower land in Tobago which was formerly clothed with seasonal forest has long since been taken up for agriculture and it is now only possible to reconstruct a conjectural picture of the original vegetation from a few relics. There is one exception to this. The small island of Little Tobago—some 280 acres—lying off the northeast coast has been protected from disturbance for over 40 years and while it is known that parts of the island were formerly cultivated it is entirely covered today with a vegetation which has all the appearance of being a climax.

While there is no rain gauge upon Little Tobago, there is no doubt that the dry season from January to May is exceedingly severe; this is clear from the most casual observation. Further the underlying geological formation is an igenous rock which has not decayed deeply and the soil is very shallow. The vegetation corresponds fairly closely in physiognomy with that of the island of Chacachacare, off Trinidad, where records show the average annual rainfall to be 48 inches, the minimum recorded annual rainfall 33 inches and the dry season to be of 5 months with under 4 inches of rain each, of which 2 have less than 1 inch.

Deciduous seasonal forest. The vegetation of Little Tobago is a deciduous seasonal forest, a formation expressing a marked deciduous period coincidental with the dry season. An unusual feature in it is the very high abundance of silver thatch palm *Coccothrinax barbadensis* (Lodd) Becc. which forms about 30 percent of the crop in both stories. This feature is absent from the formation in neighboring islands.

The forest is in two strata of which the upper is open and the lower closed. The lower story ranges from 10 to 20 feet in height and the upper story between 30 and 40 feet. The large trees branch low down and have large spreading crowns, and many shrubs of the lower story grow in clumps.

Lianes are somewhat rare though several cactaceous climbers are prominent, notably *Hylocereus Lemairei* Br. & Rose. Ground vegetation is extraordinarily sparse; grass is absent and almost the only plant is *Anthurium Hookeri* Kunth, which is also the most abundant and again almost the sole epiphyte. No trees develop buttresses normally. Only two species have thorns or spines (*Chlorophora tinctoria* and *Pithecellobium unguis-cati*); *Bursera simaruba* has a bark containing an aromatic gum.

The following are the more conspicuous components of this type, which belongs to the *Bursera-Lonchocarpus* Association (Naked Boy-Dogroot) and may be described as the Coccothrinax faciation thereof.

Upper Story.		Abundance	Evergreen or Deciduous
Silverthatch	**Coccothrinax barbadensis* (Lodd.) Becc.	v.a.	palm
Naked Boy	*Bursera simaruba* (L.) Sarg.	v.a.	D.
Dogroot	*Lonchocarpus domingensis* (Pers.) DC.	a.	D.
Banana wood	*Pisonia* sp. ? *cuspidata* Heimerl.	o.	E.
Common Cherry	*Cordia collococca* L.	o.	D.
Fiddlewood	*Citharexylum spinosum* L.	o.	D.
Parrot Apple	*Clusia* sp.	r.	E.
Hogplum	*Spondias mombin* L.	r.	D.
Fustic	*Chlorophora tinctoria* Gaud.	r.	D.

*Indentification uncertain. *C. barbadensis* is nomen confusum.

Lower Story.	(the following species in addition to young individuals of the above list.)	Abundance	Evergreen or Deciduous
Cleanteeth	*Diospyros inconstans* Jacq.	a.	E.
Black Jessie	*Pithecellobium unguis-cati* (L.) Mart.	a.	E.
Small leaf	*Eugenia ligustrina* (Sw.) Willd. and other *Myrtaceae*	a.	E.
	Trichilia trifolia L.	i.a.	E.
Wild grape	*Coccoloba* sp.	o.	E.
San Maria	*Mayepea caribaea* (Jacq.) Kuntze	o.	E.
Doctor bar	*Picramnia pentandra* Sw.	o.	E.
Rockwood	?	o.	E.
Christmas bush	*Cassia bacillaris* L. fil.	o.	E.
Torchwood	*Jacquinia barbasco* (Loefl.) Mez.	r.	E.
Money bush	*Cassia bicapsularis* L.	r.	E.
Ironwood	*Erythroxylum cumanense* H.B.K.	r.	E.
	Croton sp.	r.	D.
	Ouratea Guildingi (Planch) Urb.	r.	E.

Coccothrinax is the only palm but it forms about 30 percent of the crop in both stories. Leaving this palm out of consideration, the forest is almost entirely deciduous in the upper story and evergreen in the lower. With the bulk of the deciduous species, leaffall is always complete and takes places early in the dry season; new leaves develop at the onset of the rains. Flowering and fruiting may or may not take place during the leafless period. With *Cordia collococca* and *Citharexylum spinosum* leaffall is frequently incomplete; the crowns become less and less dense as the dry weather advances and the trees are usually almost bare just before the rains. The degree of deciduousness varies with the intensity of the

drought and in a wet year no marked leaffall may take place. Of the eight species of the upper story, the two commonest and two least common have compound leaves, the other four species simple leaves. All the species have "mesophyllous" leaves, according to Raunkiaer's leaf-size classes. In the lower story simple leaves predominate and about one-third of the species are microphyllous.

There are no local variations in the present vegetation by which one can distinguish parts of the island that were formerly cultivated from those not formerly cultivated. Evidently the succession on the formerly cleared areas is complete and the vegetation type may be described as an association rather than as an associes. Some interesting variations are, however, encountered on approaching the edge of the sea on the windward coast of the island. Among the first visible effects of exposure to the sea wind is the progressively lowering of the canopy, and the cactus *Cephalocereus moritzianus* Br. & Rose appears. Within 100 yards of the water the bush becomes windswept, neatly planed off into tables and domes, and the leaves of the palms are scorched at the edges. For the last 20 yards in many places woody plants are absent and there is a close turf of succulent herbs such as *Batis maritima* L. interspersed with clans of the Turk's Cap cactus, *Cactus Broadwayi* Br. & Rose.

Other seasonal forests. The coastal lands of Tobago are seasonally very dry and the Main Ridge is consistently wet; the intervening lands experience conditions gradually merging from one extreme to the other. It is clear therefore that before man came upon the scene, a corresponding series of transitional vegetation types must have existed, merging from the deciduous seasonal forest of Little Tobago to the lowland rain forest on the lower slopes of the Main Ridge. Such intermediate vegetation, unfortunately, has by now been almost completely destroyed, being represented only by a few small and isolated relics, mostly ruined by fellings. From these relics, however, and from assessment of habitat factors one is still able to deduce in a general way the main features of the vanished forests. On schist soil and on the alluvial soils encountered at low altitudes whether of igneous or schistose derivation, it appears that the zonation was: deciduous seasonal forest→semi-evergreen seasonal forest→evergreen seasonal forest→rain forest, which is a tropophytic clisere following the gradually diminishing severity of the seasonal drought. On leaving the coast with its deciduous seasonal forest, the canopy would rise to 60 or 80 feet and evergreen species begin to come into the upper story more prominently. This semi-evergreen seasonal forest seems to have contained *Brosimum alicastrum* Sw. (moussara), *Cedrela mexicana* Roem. (red cedar), *Cordia alliodora* (R. & P.) Cham. (cypress), *Apeiba Schomburgkii* Szyszyl. (Wild bread-nut), *Tabebuia rufescens* J. R. Johnst. and *T. serratifolia* (Vahl.) Nichols (greenheart), *Fagara martinicensis* Lam. (yellow prickle), *Citharexylum spinosum* L. (fiddlewood), *Pisonia* spp. (beefwood), *Genipa americana* L. (ibo-ink), *Spondias mombin* L. (hogplum), *Chlorophora tinctoria* Gaud. (fustic) *Erythrina pallida* Br. & Rose (beau 'mortel), *Hura crepitans* L. (sandbox) and *Coccoloba* spp. (wild grape). *Coccothrinax barbadensis* (Lodd.) Becc. may have occurred in the lower story. The next stage, evergreen seasonal forest, would be characterized by the emergence of tall outstanding trees to 120 feet above the 80 feet canopy, and the appearance of large numbers of evergreen species of the rain forest, deciduous species still being present but becoming rarer. The components here probably were *Carapa guianensis* Aubl. (crabwood), *Pachira insignis* Sw., *Licania biglandulosa* Griseb. (wild cocoa), *Lauraceae* spp. (Myers), *Cedrela mexicana* Roem. (red cedar), *Tabebuia* spp. (greenheart), *Lonchocarpus sericeus* (Poir) H. B. K. (wild yoke), *Trichilia Smithii* C.DC., *Hieronyma caribaea* Urb. (horseflesh), *Andira inermis* H. B. K. (angelin), *Spondias mombin* L. (hogplum), *Virola surinamensis* (Rol.) Warb. (wild nutmeg), *Pithecellobium jupunba* (Willd.) Urb. (soapwood), *Cordia alliodora* (R. & P.) Cham. (cypress), *Hymenaea courbaril* L. (locust), *Guarea glabra* Vahl., and *Inga* spp. (pois doux). Palms would have been represented by *Scheelea osmantha* Barb., *Roystonea oleracea* Cook and *Euterpe* sp.

On residual igneous soils the zonation was probably deciduous seasonal forest→semi-evergreen seasonal forest→xerophytic rain forest. The semi-evergreen type here seems from relics to have contained *Amomis caryophyllata* (Jacq.) Kr. & Urb. (bayleaf), *Citharexylum spinosum* L. (fiddlewood), *Tabebuia* spp. (greenheart), "Naked boy" (a large myrtaceous sp.), *Bursera simaruba* (L.) Sarg. (also called "naked boy"), *Micropholis* sp., *Fagara* spp. (yellow prickle), *Buchenavia capitata* (Vahl.) Eichl., *Cedrela mexicana* Roem. (red cedar), *Sideroxylon quadriloculare* Pierre (mastic), *Guettarda scabra* Lam. (blue copper), *Coccoloba* spp. (wild grape) and numerous myrtaceous shrubs. Palms were probably absent.

The flat plain of the lowlands was probably clothed entirely with a deciduous seasonal forest.

RAIN FORESTS

The forests on the Main Ridge are all rain forests: that is to stay they are tall evergreen forests under a climatic regime where rainfall is never scarce but is well distributed throughout the year. Further they express a habitat fairly close to the available soil-moisture optimum in the tropics, liable neither to waterlogging nor inundation nor seasonal drought. Floristically and physiognomically three distinct types can be recognized, of which one is rain forest proper, while the other two may be most conveniently regarded for the purpose of this work as belonging to sub-formations of it. In any work dealing with a larger area and including more types, lower montane rain forest would be placed in a series of montane formations and xerophytic rain forest in a group of "dry evergreen" formations which would include the littoral woodland. The three types of rain forest are:

(a) Carapa-Andira Association: rain forest proper (or more fully, tropical lowland rain forest) as described by Davis & Richards (1934) in British Guiana.
(b) Byrsonima-Licania Association: belongs to the sub-formation tropical lower montane rain forest, as described by Beard in Trinidad (1942).
(c) Manilkara-Guettarda Association: belongs to a sub-formation not hitherto described, which will be termed xerophytic rain forest.

Lowland Rain Forest

The Association is *Carapa guianensis* Aubl.-*Andira inermis* H.B.K. (Crabwood-Angelin). This is the type described by Marshall (1934) as the Carapa-Ocotea association, further information on the floristic composition having rendered the change of title desirable. This is essentially a lowland type forest and ascends only to an altitude of 800 to 1,200 feet according to exposure, so that there is relatively little of it in the Forest Reserve (see Fig. 2).

Structure. The structure is that of typical rain forest: a crowded community with large trees forming a closed canopy about 120 feet above the ground, below which two lower strata can be vaguely distinguished. Occasional outstanding trees emergent above the canopy layer such as are known in Guiana are not found here. The trees of the canopy layer, all of which have girths of 5 feet and upwards, are closely spaced and have typically very long clean straight boles, the lowest branch being usually over 60 feet from the ground. A very dense shade is cast by the canopy, so that the lower strata are not continuous and not well defined. A middle story of the forest can be vaguely distinguished between 40 and 80 feet and a lower story between 10 and 40 feet. Below this there are shrub and ground layers. Enumeration showed an average for 10 acres of 212 trees forming the canopy (the crown of each covers on the average 2,055 square feet, trees averaging 45 feet apart), 564 trees in the middle story and 834 in the lower story.

The structure is closely similar to that of rain forest in the Guianas described by Davis and Richards (1934) and by Benoist (1924).

Physiognomy and Life-form. No special study has yet been made of lianes and epiphytes in Tobago. Lianes are not particularly abundant; though every tree will have several in its crown, these are not readily noted from the ground. Epiphytes occur mainly in the crowns and do not descend lower. The greater part of the epiphytes are Bromeliaceae, of which *Aechmea dichlamydea* and *Gravisia aquilega* appear to be the most abundant. Other conspicuous species include *Guzmania lingulata* and *Vriesia longibracteata.* Most of the large trees have plank buttresses, particularly the species most characteristic of the association. There are no other peculiarities of growth to remark; no species are thorny, succulent, stilt-rooted or have peculiar bark.

The palm "mountain cabbage" (*Euterpe* sp.) is an extremely conspicuous constituent of the lower strata, representing 40 percent of the individuals in the middle story and 33 percent of those in the lower story.

Scheelea osmantha Barb. and *Roystonea oleracea* Cook. occur also but are rare to occasional. There are other palms in the shrub layer, *Bactris swordeiana* Becc. and *Geonoma* sp. The abundance of Euterpe distinguishes this association from rain forest in Trinidad and Guiana where palms are rare and found usually as immature specimens. No other special life-forms are present.

The forest is entirely evergreen save for three rare species: *Tabebuia serratifolia* (Vahl.) Nichols. (greenheart), *Ceiba pentandra* (L.) Gaertn. (silk-cotton) and *Spondias mombin* L. (hogplum), which are evidently intruders.

The commonest and most characteristic species in the upper story have compound leaves so that 55 percent of the individual trees possess this character. Pinnate arrangement is the rule. Species confined to lower strata have simple leaves.

Using Raunkiaer's leaf-size classes "mesophyllous" leaves are overwhelmingly predominant. The predominant type of mature leaf is thin and papery, dark green and shiny above with a drip-tip; that of the young leaf is pink to red-brown, limply drooping. Shrub and ground layers of the forest are only moderately dense, due to the heavy shade. There are many typical shrubs, mainly of the Rubiaceae and Melastomaceae, and ground vegetation consists of ferns and many species of herbaceous plants.

Floristic Composition. From enumeration traverses 43 species were listed in this association, counting group terms such as "small leaf" as only one species.

A list of average composition per 10 acres has been compiled from the enumeration records and appear as Table 5. In compiling this list by stories it was assumed on the basis of field observation that trees over 6 feet in girth belong to the middle story and those below 3 feet to the lower story. Twenty-three species, or just over half present, attain the canopy layer on maturity; of these the principal are:

Crabwood	*Carapa guianensis* Aubl.	v.a.	confined
Angelin	*Andira inermis* H. B. K.	a.	almost confined
Hoseflesh	*Hieronyma caribaea* Urb.	a.	do
Devilwood	*Eschweilera decolorans* Sandwith.	a.	indifferent
Wild nutmeg	*Virola surinamensis* (Rol.) Warb.	f.	confined
Soapwood	*Pithecellobium jupunba* (Willd.) Urb.	f.	indifferent
Duckwood	*Ocotea leucoxylon* (Sw.) Mez.	f.	indifferent

Carapa provides 22 percent of the trees in this story and Andira 14 percent. Of the middle story, Euterpe provides 40 percent of the trees. Young individuals of the above 7 important species of the upper story account for a further 32 percent. Important species which do not attain the upper story but are confined to this and the lower stratum are:

Wild cocoa (A)	*Licania biglandulosa* Griseb.	a.	indifferent
Wild cocoa (B)	*Marila grandiflora* Griseb.	l.a.	do
Myers	*Lauraceae* spp.	a.	do
Small-leaf	*Myrtaceae* spp.	f.	do

Species confined to the lower story are:

Wild Water-wood	*Tresanthera pauciflora* K. Schum.	a.	almost confined
Wild coffee	*Styrax glaber* Sw.	a.	indifferent
	Rudgea Freemani Sprague and Williams	f.	do
	Stylogyne lateriflora (Sw.) Mez.	f.	almost confined

It will be noted that almost all the characteristic species of the association, that is, those which are confined or almost confined to it, become large trees and form part of the canopy. Components of lower strata are mostly less restricted in distribution, due probably to the uniform conditions of forest interiors. No one family of plants is predominant here. The Leguminosae comprise only 6 percent of the individuals, in distribution to lowland Guiana and Trinidad, where the figure is from 14 to 59 percent.

Habitat. There is no doubt from general inference that the localities where this type is found represent the optimum habitat available to plant growth in Tobago. Moisture is plentiful and sufficiently abundant during the dry season to sustain growth. The association is no longer found wherever any markedly adverse factors come into play, such as on high mountain slopes exposed to wind and on shallow soils.

Lower Montane Rain Forest

Floristically the type belonging to this formation in Tobago is a faciation—which may be named the *Ternstroemia oligostemon* faciation—of the *Byrsonima spicata-Licania biglandulosa* association found also in Trinidad. The Tobago type may be referred to colloquially as Rosewood-Redwood Forest. It has not been previously described. The formation is typical of the basal regions of mountains in the tropics, representing a zone where the effects of altitude and exposure are just beginning to be felt. It has been described and defined by Beard from the mountain forests of Trinidad (1942) and the Tobago type here described is homologous. The general limits of the formation are between 400 and 2,500 feet in the Caribbean; here from 800 to 1,200 feet up to the summit of the Main Ridge, on schist soil only. The vegetation on areas of igneous soil at this altitude is the xerophytic rain forest, for reasons which will be discussed later.

Structure, Physiognomy, and Life Form. Figure 4 is a diagramatic representation of the structure in profile of this type of forest, drawn from actual measurement in the field of a suitable strip 100 feet x 25 feet. The principal respects in which it differs from lowland rain forest are:

1. The canopy is lower as a result of exposure.
2. The lowering of the canopy brings the upper and middle stories to the same height, so that there are now two strata only, an upper and a lower.
3. Buttressing is virtually absent.
4. Trees with simple leaves are predominant.

Exposure to wind has resulted in a lower canopy and a preponderance of species with simple leaves. Absence of buttresses is apparently due to better surface drainage on steeper slopes, and appears to be unconnected with the factor of wind.

The lower story, discontinuous, ranges from 10 to 40 feet and the continuous upper story from 40 to 100 feet. Trees of 4 feet girth and upwards are among those forming the canopy. Crown and stem form the same as in lowland rain forest. Enumeration showed an average for 10 acres of 276 trees forming the canopy (the crown of each covers on the average 1,580 square feet; trees averaging 40 feet apart), and 967 trees in the lower story.

The position with lianes and epiphytes is the same as in lowland rain forest, except that at high elevations, particularly along the summit of the Main Ridge, bromeliads become somewhat abundant. These have not been studied floristically. Large plank buttresses are absent. One species, *Licania biglandulosa* Griseb. may have stilt roots, particularly at higher elevations.

The palm "mountain cabbage" (*Euterpe* sp.) is still conspicuous, making up 23 percent of the lower story. In high, exposed places it is less abundant and its place is taken by *Euterpe Broadwayana* Becc.

The forest is entirely evergreen save for the rare occurrence of *Tabebuia.* Except in the case of *Simaruba amara* Aubl. which is a genuine denizen of this association, compound leaves belong only to casual intruders. Of the trees in the upper story 82 percent have simple leaves. There is considerable variation in leaf size on the same tree, leaves low down on the tree being considerably larger than those at the very top which are fully exposed to the atmosphere. The predominant size of sheltered leaves is "mesophyllous" but exposed leaves are more frequently in the "microphyll" class. The type leaf is still thin and papery though somewhat more leathery than in lowland rain forest.

The shrub layer consists mostly of Melastomes. Ground vegetation is usually fairly sparse, consisting of seedlings, a few ferns and herbaceous plants. Tree ferns are not represented in Tobago except by a few small Alsophilas.

Along the summits of the Main Ridge and its lateral ridges, the added exposure reduces the canopy to some 60 feet, the forest becoming more open, mossy, with abundance of *Euterpe Broadwayana* and bromeliads, the latter frequently terrestrial, and a lush ground vegetation.

Floristic Composition. In passing from lowland to lower montane rain forest there is no radical change of flora. Much the same species occur, but their relative abundance is different. From enumera-

tion traverses in the Byrsonima-Licania association a total of 50 species was recorded, counting group terms as one each, of which six could not be identified at least as far as genus. The flora high up in the mountains has not been so well collected and is not so well known locally; no creole names could be elicited for 16 of the 50 component species. A list of average composition per 10 acres appears as Table 6. Thirty species may on maturity attain the upper story, of which the principal are:

Rosewood	*Byrsonima spicata* Rich.	v.a.	almost confined
Wild cocoa (A)	*Licania biglandulosa* Griseb.	a.	indifferent
Redwood	*Ternstroemia oligostemon* Kr. & Urb.	a.	almost confined
Devilwood	*Eschweilera decolorans* Sandwith	a.	indifferent
"Red" Lionwood	*Sloanea trinitensis* Sandwith	a.	almost confined
Bitter Quassia	*Simaruba amara* Aubl.	f.	almost confined

Licania and Eschweilera are conspicuous constituents of the Carapa-Andira association, but the four other species above occur only casually elsewhere. Other species characteristic of this association are a *Sloanea* sp. close to *S. trinitensis* ("White" Lionwood), *Richeria grandis* Vahl., *Sloanea Purdiaei* Griseb., and three unknown species referred to as "Redbark," "Wartybark," and "Red polish."

Twenty species are small trees which do not rise above the lower story. The principal of these are:

Mountain cabbage (A)	*Euterpe* sp.	l.v.a.	indifferent
Small-leaf	*Myrtaceae* spp.	a.	do
Mountain cabbage (B)	*Euterpe Broadwayana* Becc.	l.v.a.	do
Wild coffee	*Styrax glaber* Sw.	a.	do
	Rudgea Freemani Sprague and Williams	o.	do
Wild cocoa (B)	*Marila grandiflora* Griseb.	l.f.	do

All the above are "indifferent" species; several are of localized distribution. The Euterpe "mountain cabbage" is the only palm in sheltered situations, but is replaced by *E. Broadwayana* in exposed places. The former often gregariously occurs in patches which probably have been gaps in the forest caused by wind damage. Marila keeps to the banks of watercourses.

The characteristic species of the Carapa-Andira association (*Carapa guianensis, Andira inermis, Hieronyma caribaea,* and *Virola surinamensis*) are here only casuals, usually in sheltered situations on the banks of streams. The change-over from the one association to the other is usually fairly abrupt.

At the lower levels, Byrsonima and Ternstroemia are clearly dominant, but high up their abundance is reduced somewhat relative to *Eschweilera, Licania, Ocotea,* and *Sloanea* spp. *Richeria grandis* is a prominent species confined to upper altitudes. On the crest of the Main Ridge and similar places of maximum exposure, *Licania biglandulosa* is dominant with *Euterpe Broadwayana, Richeria grandis,* and *Erythroxylum impressum.*

There is no predominant family, Leguminosae comprising less than 2 percent of the trees.

Habitat. It has already been shown how the habitat of this type differs from that of lowland rain forest, namely in respect to greater exposure to wind, lower temperature, and higher and more constant rainfall.

It should be noted that lower montane rain forest in Tobago occurs only on soil derived from schist and not on igneous soil. The schist soil is a deep clay, parent rock having decayed usually to a depth of several feet. Igneous soil at a like altitude is extremely shallow and apparently for this reason xerophytic rain forest is found upon it.

Xerophytic Rain Forest

The association is characterized by *Manilkara bidentata* (A.DC.) Chev. and *Guettarda scabra* Lam. (Gooseberry-Blue Copper). Marshall (1934) notes this type as a Calophyllum-Mimusops (Manilkara) associes and regards it as a "deflected climax," whereas the writer prefers to regard it as virgin forest; this question is discussed below under "habitat."

This formation is found on igneous soil only, above 800 feet altitude; in high places where the soil is shallow and externally well drained and where there is the maximum exposure to wind.

Structure. The structure differs rather radically from that of the other rain forests (Fig. 5). Two tree strata can be defined. A more or less continuous canopy is found between 40 and 60 feet; below this the smaller trees are not arranged in any definable layers, but above the canopy occasional solitary large emergent trees stand out up to 90 feet in height.

The emergents occur at the average rate of 10 per acre (98 per 10 acres, from enumeration)—equal to 66 feet apart—though the distribution is not constant. They may attain very large sizes of over 12 feet in girth. Trees of the canopy layer and lower levels occur at the rate of 1,335 per 10 acres and seldom attain girths of over 3 feet. The overwhelming proportion of the forest, therefore, is composed of trees not exceeding 12 inches in diameter, which gives the impression of a small pole crop. Many of these trees have long, thin, straight boles and restricted crowns; others branch or fork low down.

The most regular structure is found on southern and eastern slopes and on the tops of ridges (except at the highest altitudes). Here the largest emergents are found and the canopy is quite regular. On western aspects a combination of windthrow and soil creep has frequently destroyed any regular structure, the canopy being full of gaps; emergents are usually absent.

Physiognomy and Life-Form. This formation exhibits a number of somewhat peculiar features which seem indicative of a general xerophytism. These are not, however, the features associated with the xerophytism of seasonal scarcity of rainfall: deciduousness, microphylly, thorniness and succulence. None of these is present. The forest is entirely evergreen —except for one rare species, *Tabebuia serratifolia*

in the lower layers—predominantly mesophyllous and without thorns or succulents. The actual features referred to appear in the leaves and bark, the predominant species possessing leaves which are thick and fleshy or thickly cutinized or contain an essential oil, and having the habit of shedding their bark. The former character belongs particularly to the emergents and the latter to the lower layers. This may be demonstrated mathematically as follows:

Character	Emergent Trees		Lower Layers	
	Number of Species	Percentage of Individuals	Number of Species	Percentage of Individuals
1. Leaf with thick cuticle or waxy indumentum......	3	57	9	28
2. Leaf containing aromatic oil......	..	0	1	5
3. Coniferous type leaf............	1	17	1	4
4. Leaf thick and fleshy............	1	8	2	13
Total with specialized leaves.......	5	82	13	50
5. Bark shedding....	..	0	6	42

The 9 species with cutinized leaves are *Manilkara bidentata, Micropholis cruegeriana, Calophyllum lucidum, Myrtaceae* spp. (small-leaf), *Ternstroemia oligostemon, Eugenia confusa, Ficus* sp., and *Mouriri rhizophoraefolia. Amomis caryophyllata* and several other Myrtaceae contain an essential oil in their leaves. *Podocarpus coriaceus* is the conifer. *Clusia rosea* and *Cassipourea latifolia* have thick fleshy leaves.

The bark-shedders are *Guettarda scabra, Myrtaceae* spp., *Amomis caryophyllata, Chione venosa, Eugenia confusa*, and *Mouriri rhizophoraefolia.* All these species have a very smooth thin bark which peels off in papery sheets. Species of the family *Myrtaceae* (except *Amomis*) peels off in small flakes, but Guettarda, Amomis, and Chione peel in quite large sheets. In all cases the bark has a shaggy appearance and piles of shed bark accumulate around the base of the tree. The striking appearance of this phenomenon is increased by the color effects; peeling sheets of bark are often whitish or pale-brown whereas newly exposed underbark shows, according to species, all colors from greenish-white to purple or brilliant fleshy orange. The whole effect is bizarre in the extreme, heightened by the strange stem-form of the bark-shedding species whose trunks are seldom cylindrical but irregularly lobed, often to an exaggerated degree in old trees.

The combination of the small stature of the forest, the peculiarities of leaf and the bark-shedding habit is strongly suggestive of xerophytism, representing lack of available moisture. It is impossible to say what actual effects these structural phenomena have. We do not know whether they effectively reduce transpiration or assist by any other means toward the endurance of an unfavorable habitat. The association of so many of these strange trees in a dwarf forest in this locality is at any rate highly suggestive.

Lianes are virtually absent here and epiphytes relatively scarce, bromeliads only being noticed. Razor grass (Scleria) is abundant in windfall gaps, particularly in the poorer forest of the eastern aspects.

Palms are confined to the phase of eastern aspects where they appear in gaps. As is found elsewhere, *Euterpe Broadwayana* occurs at high and the other Euterpe at low levels.

Only three species here have compound leaves, constituting 4 percent of the emergents and 2 percent of the lower strata; they are all casuals. The predominant leaf type is simple, mesophyllous and in some manner specialized.

There is no shrub layer here and ground vegetation is typically sparse; a thick humus mat, a few seedlings and some coarse grass.

Floristic Composition. The association contains a number of interesting floristic features, due to the specialization of the habitat. In Table 7 is given a list of average composition per 10 acres, from enumeration records. Counting as usual group terms as one each, 36 species only were recorded, of which 6 "eluded" even approximate identification. The figure of 36 species seems to indicate a poor flora. The bulk of the Myrtaceae, however, have been counted under a group-term as one (small-leaf), but they are a particularly well developed group here and if later they can be further differentiated in the field the total of species will be substantially added to. Eleven of the component species may grow as emergents, the balance of 25 being confined to lower levels.

This association is of rather more variable composition than the others described. There are in fact two distinct phases, the more widespread of which occurs on ridge tops and on south and east aspect slopes (that is, wherever most exposed to the wind) and the other on westerly aspects where to some extent sheltered. In the former case, the principal emergent trees are:

Gooseberry.......	*Manilkara bidentata* (A.DC.) Chev..........	v.a.
Galba...........	*Calophyllum lucidum* Benth................	a.
Parrot apple......	*Clusia rosea* Jacq..................	f.
....	*Micropholis Cruegeriana* Pierre............	f.
....	*Licania ternatensis* Hook f................	f.
....	*Roupala montana* Aubl..................	o.

The lower strata are additionally composed of:

Blue Copper......	*Guettarda scabra* Lam....................	v.a.
Small-leaf........	*Myrtaceae* spp..........................	a.
Bayleaf..........	*Amomis caryophyllata* (Jacq.) Kr. & Urb.....	a.
....	*Cassipourea latifolia* Alston................	f.
....	*Chione venosa* (Sw.) Urban................	f.
....	*Erythroxylum impressum* O. E. Schultz.......	o.

Podocarpus coriaceus Rich. is absent except at very high levels where it may become occasional. In this phase bark-shedding trees are particularly prominent.

On western aspects, the principal emergents are:

	Podocarpus coriaceus Rich.	a.
Parrot apple	*Clusia rosea* Jacq.	f.
	Roupala montana Aubl.	f.
Bitter Quassia	*Simaruba amara* Aubl.	o.
	Licania ternatensis Hook f.	o.

and additionally in the lower levels,

Small-leaf	*Myrtaceae* spp.	a.
	Cassipourea latifolia Alston	f.
"Pinkbark"	?	f.
Mountain cabbage (B)	*Euterpe Broadwayana* Becc.	l.a.
Mountain cabbage (A)	*Euterpe* sp.	l.f.

Conspicuous absentees here are Manilkara, Calophyllum, Guettarda, and Amomis. Bark-shedding trees are inconspicuous and palms are present.

Licania biglandulosa Griseb. (wild cocoa) becomes abundant in zones of transition to adjoining forest of the Carapa-Andira type.

A conspicuous feature of the association in general is the high degree of exclusiveness among the more abundant species. Of the emergent trees, *Manilkara bidentata, Podocarpus coriaceus,* and *Licania ternatensis* were not recorded elsewhere in Tobago and appear confined to the association, while *Clusia rosea, Micropholis Cruegeriana, Calophyllum lucidum,* and *Roupala montana* are virtually confined to it. Similarly in the lower strata *Guettarda scabra, Amomis calyophyllata,* "Pinkbark," *Chione venosa,* and *Mouriri rhizophoraefolia* are confined to the association, and *Cassipourea latifolia* and *Eugenia confusa* virtually confined.

There is no predominant plant family. Only one leguminous species was recorded and that as rare. The bark-shedding trees do not belong to any one family but are distributed among the Myrtaceae, Rubiaceae, and Melastomaceae.

Habitat. The specialized features exhibited by the vegetation may assist one in deducing the essential features of the habitat. "Xerophytic Rain Forest" may at first sight appear to be a contradiction in terms; however, while the forest is "rain" forest—for rainfall in this zone has been observed to be more or less consistently plentiful all the year round—yet it seems that there is a scarcity of available soil moisture. We may probably legitimately infer a scarcity of moisture from the low, poor growth of the trees and the concentration of species with certain structural peculiarities may imply this. To attempt to decide the cause of this lack of moisture is not altogether easy. Most likely the shallowness of the soil is responsible. The writer observed that tree roots seldom penetrate much below 18 inches in depth, which may be because the rotten rock below is too hard and resistant or because some factor of chemical toxicity is present. On the steep mountain slopes the shallow upper layer to which the roots are confined must dry out very rapidly between rain showers, particularly as the soil is porous and the area exposed and windy.

Marshall (1934), while admitting the lack of precise knowledge, tentatively classified this type as a deflected or biotic climax because it is "dissimilar from the other forests found in the vicinity" and because "from the history of Tobago it is more than likely that this zone was once under cultivation." The present writer finds no evidence to support the latter statement; rather does it appear that the bulk at any rate of this zone never has been under cultivation. Pigeon Hill, now included in the Forest Reserve, was private land up to 1912 and was very probably cultivated at one time but is covered today with forest belonging quite characteristically to the Byrsonima-Licania association. This consideration apart, the conception of the "biotic climax" embraces a type of secondary vegetation which is prevented from returning to the original virgin type by the continual operation of some human factor or by some permanent alteration of the habitat caused by human interference. The active human factor may be fire, grazing, or felling: here fires appear to be unknown, there is no grazing, nor is there felling because this association contains virtually none of the timber trees now commonly worked in Tobago. Soil erosion might have caused a permanent change in conditions, but none of the soil profiles examined were truncated. The evidence certainly suggests that this is no biotic climax.

It might, on the other hand, be contended that this is a seral community in a state of development after human destruction. It contains, however, a number of very large trees, which must be of great age, perhaps 200 years, belonging to species absolutely confined to this area. It seems easier, having regard to all the facts, to explain this type as a natural community.

SUMMARY

The communities of natural vegetation in Tobago have been described and classified as follows:

Formation	Association	Area on C.L. (acs.)
1. Mangrove Woodland	*Rhizophora mangle-Avicennia nitida-Laguncularia racemosa*	—
2. Littoral Woodland	*Hippomane mancinella-Coccoloba uvifera*	60
3. Deciduous Seasonal Forest	*Bursera simaruba-Lonchocarpus domingensis*	280
4. Rain Forest:		
(a) Lowland Rain Forest	*Carapa guianensis-Andira inermis*	3,920
(b) Lower Montane Rain Forest	*Byrsonima spicata-Licania biglandulosa*	8,330
(c) Xerophytic Rain Forest	*Manilkara bidentata-Guettarda scabra*	1,980
		14,570

The following summarizes the habitat moisture relations of the above types:

EDAPHIC

Swamp formation:

Mangrove woodland. Soil tidally inundated with brackish water (physiological drought).

CLIMATIC

Seasonal formation:

Deciduous seasonal forest. Severe lack of soil moisture during 5 months of dry season due to irregular precipitation.

Dry evergreen formations:

Littoral woodland, xerophytic rain forest. Available moisture inadequate due to shallow rocky soil and very high atmospheric evaporation.

Montane formation:

Lower montane rain forest. Available moisture to some extent inadequate due to lowered temperature and high atmospheric evaporation on clear days.

Optimum formation:

(Lowland) rain forest. Moisture conditions ideally favorable.

TABLE 8. Provisional list of native trees recorded from Tobago.

NOTE: For the purposes of this list, a tree is assumed to be a woody plant growing on maturity to a height of over 15 feet and a diameter of over 4 inches. Creole names are given where known and are of local origin except where shown in brackets: these indicate a Trinidad name which has crept into use in default of a Tobago name. The families are arranged in Bentham and Hooker order so as to follow the Flora of Trinidad and Tobago. The symbol ! indicates that the species has not been previously recorded in the Flora or represented in the Trinidad Herbarium.

GYMNOSPERMAE.	
CONIFERAE	
Podocarpaceae	
Podocarpus coriaceus Rich.	
ANGIOSPERMAE.	
I. DICOTYLEDONES	
1. Annonaceae	
Anaxagorea acuminata St. Hil.	Burn-nose
Duguetia tobagensis (Urb.) R.E. Fr.	
2. Hypericaceae	
Vismia cayennensis Pers.	Yellow wattle
Vismia falcata Rusby.	
3. Guttiferae	
Calophyllum lucidum Benth.	Galba
Clusia minor L.	
Clusia palmicida Rich.	Parrot apple
Clusia rosea Jacq.	
Marila grandiflora Gr.	Wild cocoa
4. Theaceae	
Ternstroemia oligostemon Kr. & Urb.	Redwood
5. Malvaceae	
Pariti tiliaceum (L.) Juss.	Seaside mahoe
Thespesia populnea (L.) Soland.	
6. Bombacaceae	
Ceiba pentandra (L.) Gaertn.	Silk Cotton
Ochroma pyramidale (Cav.) Urb.	Bois flot
Pachira insignis Sw.	Wild breadnut
7. Sterculiaceae	
Guazuma ulmifolia Lam.	Pigeon wood
8. Tiliaceae	
Apeiba Schomburgkii Szyszyl.	Wild breadnut
! *Sloanea Purdiaei* Gr.	Tobago yoke
! *Sloanea trinitensis* Sandwith	"Red" Lionwood
Sloanea sp.	"White" Lionwood
9. Ochnaceae	
Ouratea Guildingi (Planch.) Urb.	
10. Erythroxylaceae	
! *Erthroxylum cumanense* H.B.K.	Ironwood
! *Erythroxylum impressum* O. E. Schultz.	
Erythroxylum ovatum Cav.	
11. Malpighiaceae	
Byrsonima spicata Rich.	Rosewood
12. Rutaceae	
Esenbeckia pilocarpoides H.B.K.	
! *Fagara martinicensis* Lam.	Yellow prickle
13. Burseraceae	
Bursera Simaruba (L.) Sarg.	Naked boy
14. Simarubaceae	
Picramnia pentandra Sw.	Doctor bar
Simaruba amara Aubl.	Bitter Quassia, Marouba, Boardwood
15. Meliaceae	
! *Carapa guianensis* Aubl.	Crabwood
Cedrela mexicana Roem.	Red cedar
! *Guarea glabra* Vahl.	
Trichilia trifolia L.	
Trichilia Smithii DC. (*T. oblanceolata* Rusby)	
16. Sapindaceae	
Cupania americana L.	
! *Dodonaea viscosa* L.	
Matayba arborescens Radlk.	
17. Anacardiaceae	
Spondias Mombin L.	Hogplum
18. Papilionatae	
Andira inermis H.B.K.	Angelin, Black plum
Erythrina pallida Br. & Rose	Beau 'mortel
Lonchocarpus domingensis (Pers.) DC.	Dogroot
Lonchocarpus sericeus (Poir.) H.B.K.	Wild yoke
19. Caesalpinieae	
Brownea latifolia Jacq.	Tobago beau
Cassia bacillaris L. fil.	Cocrico bush
Cassia bicapsularis L.	Money bush
Crudia obliqua Gr.	
Hymenaea courbaril L.	Locust
20. Mimoseae	
Albizzia caribaea (Urb.) Br. & Rose	Tantacayo
Inga edulis Mart.	
Inga macrophylla H. & B.	(Pois doux)
Inga punctata Willd.	
Pithecellobium jupunba (Willd.) Urb.	Soapwood
Pithecellobium unguis-cati (L.) Mart.	Black Jessie
21. Rosaceae	
Chrysobalanus icaco L.	Fat pork
Hirtella racemosa Lam.	
Hirtella silicea Gr.	
Licania biglandulosa Gr.	Wild Cocoa
Licania Cruegeriana Urb.	
Licania ternatensis Hook f.	
Moquilea leucosepala (Gr.) R. O. Williams	
22. Rhizophoraceae	
Cassipourea latifolia Alston	
Rhizophora Mangle L.	Mangrove
23. Combretaceae	
! *Buchenavia capitata* (Vahl.) Eichl.	Yellow sanders
Conocarpus erectus L.	Mangrove
Laguncularia racemosa (L.) Gaertn.	Mangrove
24. Myrtaceae	
Amomis caryophyllata (Jacq.) Kr. & Urb.	Bay leaf
Calyptranthes sericea Gr.	
Eugenia albicans (Berg.) Kr. & Urb.	
Eugenia confusa DC.	
Eugenia Cruegeri Kr. & Urb.	
Eugenia ligustrina (Sw.) Willd.	
Eugenia monticola (Sw.) DC.	
! *Krugia ferruginea* (Poir.) Urb.	Small-leaf
Myrcia Berberis DC.	
Myrcia dumosa (Berg.) Kr. & Urb.	
Myrcia leptoclada DC.	
Myrcia splendens (Sw.) DC.	
Myrcia tobagensis (Kr. & Urb.) Urb.	
25. Lecythidaceae	
Eschweilera decolorans Sandwith.	Devilwood
26. Melastomaceae	
Miconia guianensis (Aubl.) Cogn.	
Miconia laevigata (L.) DC.	Wild spice
Miconia racemosa (Aubl.) DC.	
Mouriri rhizophoraefolia (DC.) Triana	

TABLE 8. *(Continued)*

27. Samydaceae	
Casearia decandra Jacq.	
Casearia guianensis (Aubl.) Urb.	
Casearia spinescens (Sw.) Gr.	
Casearia sylvestris Sw.	
28. Cactaceae	
Cephalocereus Moritzianus (Otto.) Br. & Rose	
29. Rubiaceae	
Basanacantha phyllosepala Sprague & Williams	
! *Chimarrhis cymosa* Jacq.	Waterwood
Chione venosa (Sw.) Urban	
Faramea occidentalis (L.) A. Rich.	
Genipa americana L.	Ibo-ink
Guettarda parviflora Vahl.	Blue copper,
Guettarda scabra Lam.	Poor man candle
Guettarda tobagensis Urb.	
Psychotria pinnularis Moç. & Sessé	
Psychotria tobagensis Urb.	
Psychotria uliginosa Sw.	
Randia aculeata L.	
Rudgea Freemani Sprague & Williams	
Tresanthera pauciflora K. Schum.	Wild waterwood
30. Myrsinaceae	
Conomorpha peruviana DC.	
Stylogyne lateriflora (Sw.) Mez.	
Weigeltia antillana Mez.	
31. Theophastaceae	
Jacquinia barbasco (Loefl.) Mez.	Torchwood
Jacquinia revoluta Jacq.	
32. Sapotaceae	
! *Bumelia buxifolia* Willd.	
Chrysophyllum argenteum Jacq.	
! *Manilkara bidentata* (A.DC.) Chev.	Gooseberry, (Balata)
Micropholis Cruegeriana Pierre	
Sideroxylon quadriloculare Pierre	Mastic
33. Ebenaceae	
Diospyros inconstans Jacq.	Clean-teeth
34. Styracaceae	
! *Symplocos martiricensis* Jacq.	
! *Styrax glaber* Sw.	
35. Oleraceae	
Linociera caribaea (Jacq.) Knobl.	San Maria
36. Apocynaceae	
Tabernaemontana oppositifolia (Spreng.) Urb.	
37. Boraginaceae	
Bourreria succulenta Jacq.	
Cordia alliodora (R. & P.) Cham.	Cypress
Cordia collococca L.	Common cherry
Cordia spp.	Wild manjack
38. Bignonaceae	
Tabebuia rufescens J. R. Johnst.	Greenheart, Cogwood
Tabebuia serratifolia (Vahl.) Nichols	
39. Verbenaceae	
Avicennia nitida Jacq.	Mangrove
Citharexylum spinosum L.	Fiddlewood
Vitex divaricata Sw.	Timber fiddlewood
40. Nyctaginaceae	
! *Pisonia cuspidata* Heimerl.	Beefwood
Pisonia Eggersiana Heimerl.	Banana wood
41. Polygonaceae	
Coccoloba latifolia Lam.	Wild grape
Coccoloba uvifera L.	Sea grape
42. Myristicaceae	
Virola surinamensis (Rol.) Warb.	Wild nutmeg
43. Lauraceae	
Aniba panurensis Mez.	
Nectandra membranacea (Sw.) Griseb.	
Ocotea leucoxylon (Sw.) Mez.	Duckwood, Black cedar
Phoebe elongata (Vahl.) Nees.	
44. Thymelaeaceae	
Daphnopsis caribaea Griseb.	
45. Hernandiaceae	
! *Hernandia sonora* L.	
46. Proteaceae	
Roupala montana Aubl.	
47. Euphorbiaceae	
Alchornea glandulosa Poepp.	
Croton gossypifolius Vahl.	Bloodwood
Hieronyma caribaea Urb.	Horseflesh
Hippomane mancinella L.	Manchineel
Hura crepitans L.	Sandbox
Richeria grandis Vahl.	
Sapium aucuparium Jacq.	
48. Moraceae	
Brosimum alicastrum Sw.	Moussara
Cecropia peltata L.	Trumpet tree
Chlorophora tinctoria Gaud.	Fustic
Ficus tobagensis Urb.	Bowldish, Wild milking
Ficus grenadensis Warb.	
Ficus Hartii Warb.	
Trema micranthum (L.) Blume	
II. MONOCOTYLEDONES	
Palmae	
Acrocomia ierensis L. H. Bailey	Shac-shac tree
Bactris Sworderiana Becc.	Samson wood
Coccothrinax barbadensis (Lodd) Becc.	Tobago fan palm, silverthatch
Euterpe Broadwayana Becc.	Mountain cabbage
Euterpe sp.	
Geonoma sp.	Anaré, Gully palm
Roystonea oleracea Cook	Cabbage palm
Scheelea osmantha Barb.	Rough palm, One man

TABLE 9. Key to index letters on profile diagrams in Figures 7 and 10.

Index letter	Species	No. in X.R.F.	No. in L.M.R.F.
A	*Amomis caryophyllata* (Jacq.) Kr. & Urb.	1	–
B	*Byrsonima spicata* Rich.	–	3
C	*Cassipourea latifolia* Alston	6	–
Ch	*Chione venosa* (Sw.) Urban	3	–
E	*Eugenia* and *Myrcia* spp.	2	7
Eg	*Euterpe* sp.	–	1
Er	*Erythroxylum impressum* O. E. Schulz	3	1
G	*Guettarda scabra* Lam.	2	–
K	*Krugia ferruginea* (Poir.) Urb.	1	–
Lb	*Licania biglandulosa* Griseb.	–	10
Lt	*Licania ternatensis* Hook f.	7	–
M	*Manilkara bidentata* (A.DC.) Chev.	1	–
Mi	*Miconia* sp.	–	1
R	*Richeria grandis* Vahl.	–	1
Ro	*Roupala montana* Aubl.	1	–
Sl	*Sloanea trinitensis* Sandwith	–	1
S	*Styrax glaber* Sw.	–	3
Ta	*Tabebuia serratifolia* (Vahl.) Nichols	1	–
Te	*Ternstroemia oligostemon* Kr. & Urb.	–	2
?	Unknown	–	2

LITERATURE CITED

Beard, J. S. 1942. Montane Vegetation in the Antilles. Caribbean Forester **3**: 61-74.

Benoist, R. 1924. La Vegetation de la Guyane Française. Bull. Soc. Bot. de France **71**: 1169-1777 (in French).

Broadway, W. E. 1916. The Palms of Tobago. Bull. Dept. Agri., Trinidad 15, p. 174.

Charter, C. F. 1941. A Reconnaissance Survey of the Soils of British Honduras. Govt. Printer, Trinidad, B. W. I. 31 pp.

Cunningham-Craig, E. H. 1907. Preliminary Report on Geology of Tobago. Council Paper No. 9 of 1907. Govt. Printer, Trinidad.

Davis, T. A. W., & Richards, P. W. 1934. The vegetation of Moraballi Creek, British Guiana. Jour. Ecology **21:** 350-384, **22:** 106-155.

Hardy, F., Akhurst, G. G., & Griffith, G. 1931. The cacao soils of Tobago. III of Studies in West Indian Soils. Govt. Printer, Trinidad, B. W. I. 22 pp.

Marshall, R. C. 1934. Physiography and Vegetation of Trinidad and Tobago. Oxford Forestry Memoir 17. Univ. of Oxford.

Sandwith, N. Y. 1938. Notes on the Flora of Tobago. 37 of Contributions to the Flora of Tropical America, Kew Bulletin of Misc. Information.

Swabey, C. The Palms of Trinidad and Tobago. (Unpublished.)

Trechmann, C. T. 1934. Tertiary and Quaternary Beds of Tobago. Geo. Mag. **71:** 481-493.

Williams, R. O., & Cheesman, E. E. 1928-41. Flora of Trinidad and Tobago (incomplete). Govt. Printer, Trinidad, B. W. I. Pp. 1-464 (part I) and 1-122 (part II).

SOME RODENT POPULATIONS IN THE SIERRA NEVADA OF CALIFORNIA

TRACY I. STORER, FRANCIS C. EVANS, AND FLETCHER G. PALMER

Contribution from the Division of Zoology,
College of Agriculture, University of California
Davis, California

TABLE OF CONTENTS

SOME RODENT POPULATIONS IN THE SIERRA NEVADA OF CALIFORNIA

INTRODUCTION

Rodents constitute one of the major dynamic forces of nature; they are second only to the insects, and well above the hoofed animals, wild and domestic, as primary converters of vegetation; they provide the staple food of many carnivorous animals, including useful fur bearers and harmful predators; over a large part of the earth they are the largest component of the animal kingdom, both as to species and numbers of individuals excepting insects; and they form an important reservoir for diseases that may be transmitted to man, to his domestic animals, and to other wild species. Because of these and other features they are one of the major factors in the economic life of man, particularly in western North America.

Despite the important relations of rodents to agriculture, public health, wildlife conservation, recreation, and other fields of man's interests, there has been surprisingly little direct research on the native species. Rodent control operations, past and present, have involved huge expenditures—a half million dollars or more annually in California alone, in recent decades. Small sums have been spent on the study of control methods; in California this has amounted to about one per cent of the control expenditures in recent years. Somewhat larger amounts have been provided for surveys of disease in rodents. But almost nothing has been set aside for actual study of the animals themselves.

Investigations on the natural history of rodents involved as vectors of diseases transmissible to man were organized under the joint auspices of the California State Department of Public Health and the Hooper Foundation and College of Agriculture of the University of California. These were carried on from May 19 to October 31, 1937, about Lake Tahoe, California, by F. G. Palmer, and produced a few quantitative data and more of a qualitative character regarding the rodents of a mountain region heavily utilized by summer vacationists. The results were so encouraging that a more intensive program was outlined for the next season, under the same agencies and aided by funds from the Social Security Board. The field party consisted of Charles M. Wheeler, Fletcher G. Palmer, and Robert H. Peters. It was hoped that this group might return to the Lake Tahoe region, but it was found necessary to select a new site near Bass Lake (The Pines P. O.), Madera County, California. Work was carried on there from July 6, 1938 until July 8, 1939, although only occasional records were made between January 6 and March 22, when the study area proved to be inaccessible (Fig. 1).

FIG. 1. Outline of California to show locations of the two study areas.

Acknowledgments are due the California Department of Public Health for arranging the facilities under which the studies were conducted; the Hooper Foundation for Medical Research, for supplying a considerable part of the necessary equipment; Dr. S. B. Benson, of the Museum of Vertebrate Zoology, for lending live traps for a portion of the study; and the U. S. Forest Service for weather records of two localities near Bass Lake (Northfork, 2700 feet altitude, and Miami Station, 4800 feet). Mrs. Emily P. Thompson prepared the line figures. The authors are under obligation to Dr. K. F. Meyer for the use of the original records of the survey in preparing this report.

LAKE TAHOE: 1937

Lake Tahoe (Fig. 2) lies near the crest of the Sierra Nevada, its surface being 6,225 feet above sea level. Its shores and the adjacent slopes are favored as recreational areas by several thousand persons every summer. The summer climate includes warm days, occasional thundershowers, often strong winds, and usually cool nights. In winter much of the region is well blanketed with snow.

The environs of the lake are largely granite, with some areas of lava rock. Biologically the region belongs to the arid high Transition and Canadian life zones. The principal vegetational cover is forest, of Jeffrey pine, sugar pine, lodgepole pine, incense cedar, white fir, western juniper, and black oak, with much montane chaparral that includes *Arctostaphylos patula, Quercus vaccinifolia, Ceanothus cordulatus, Cast-*

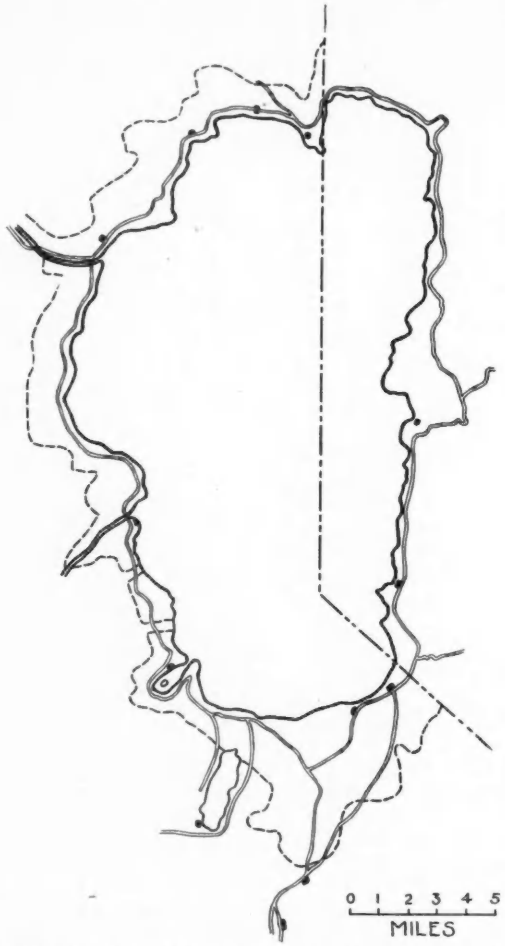

FIG. 2. Outline of Lake Tahoe (heavy lines), with principal roads (parallel lines) and approximate limits of area poisoned in plague control operations during 1937 (broken lines); no data for the Nevada side.

anopsis sempervirens, Prunus emarginata, Artemisia tridentata, and other species. Dry flats supported large growths of a "sunflower," *Wyethia mollis.* There are scattered meadows, chiefly at the north and south ends of the lake.

Several species of rodents often live in or about houses, cabins or other buildings around Lake Tahoe. The commonest is the deer mouse *(Peromyscus maniculatus).* Another species of deer mouse *(Peromyscus boylii)* and the bushy-tailed wood rat *(Neotoma cinerea)* occur around buildings situated within their preferred habitats. The house mouse *(Mus musculus)* is found locally, chiefly in cabins. Chipmunks also enter buildings, especially if the latter are poorly constructed or are unoccupied. Several kinds of rodents nest commonly under buildings and run about on the porches and nearby woodpiles; these include the golden-mantled ground squirrel *(Citellus lateralis)*, chipmunks *(Eutamias amoenus, E. quadrivittatus,* and *E. quadrimaculatus),* and the chickaree *(Sciurus douglasii).* Common in yards and sometimes living under buildings or woodpiles are two ground squirrels *(Citellus beecheyi* and *C. beldingi).*

A few instances of relapsing fever and of sylvatic plague have been found in the region, among both rodents and human beings, and although the hazard of infection from rodents does not appear to be great, control measures were deemed necessary. During the summer of 1937 poisoned grain was distributed by county and state officials on lands surrounding Lake Tahoe (Fig. 2). This afforded an opportunity to study rodent populations on poisoned areas and to make some determinations of the rate of reinvasion of rodents into such areas.

METHODS

The Tahoe rodent studies served mainly to develop methods for population censuses. Visual counts were tried with Belding ground squirrels but did not prove satisfactory and were not practicable with other species. Permanent and moving lines of snap traps were employed to remove all rodents from small areas to estimate the local populations and, by repetition at intervals, to learn the extent of reinvasion. Because of local movements by rodents from closely adjacent areas, these trap lines provided little reliable information on actual population densities. Recourse was had later in the season to live traps which made possible the capture, marking, and release of rodents for more accurate estimates of populations.

An integral part of these studies was the collection of fleas to determine (1) the species present on the several rodent hosts; (2) the flea-index as to numbers per rodent; (3) the presence or absence of plague organisms within the fleas; and (4) the rate at which a rodent acquires new fleas after those present have been removed. The data for items 1, 2 and 4 are being worked up by M. A. Stewart; those for item 3 have been reported by K. F. Meyer (1938). The rodents were taken in live traps and each animal was marked for subsequent identification. Rounds of the traps were made once each morning and twice each afternoon. With each individual the procedure was as follows: the animal was forced from the trap into a large wide-mouthed glass fruit jar, a lid was put on, and, with an atomizer, chloroform was sprayed in through a small hole in the lid. When just "under" the anesthetic, the rodent was turned into a large aluminum roasting-pan with 6-inch sides. Its hair then was combed thoroughly to remove all fleas; the cotton in the trap and the inside of the jar also were examined for fleas. Specimens so obtained were placed in small vials of normal saline solution, using a separate vial for those from each species of rodent.

TRAPPING EXPERIMENTS

Elimination trapping was employed in the first experiment to measure population density. At a site

2 miles southwest of Myers, covered by short grass, sparse sagebrush and some lodgepole pines, an area of 0.78 acre was "trapped out" on three successive occasions; 38 to 40 rat traps were kept going in each case until no rodent was taken for 3 successive days. Trapping was then suspended for several weeks and later resumed. The results were as follows:

	June 8-26		Aug. 2-17		Sept. 27-Oct. 9	
	Actual Number	Per Acre	Actual Number	Per Acre	Actual Number	Per Acre
Citellus beecheyi	0	0	2	2.6	0	0
Citellus beldingi	3	3.8	11	14.1	*	*
Citellus lateralis	4	5.1	17	21.8	5	6.4
Eutamias amoenus	7	9	17	21.8	1	1.3
Eutamias quadrivittatus	16	20.5	16	20.5	0	0
Sciurus douglasii	0	0	1	1.3	1	1.3
Peromyscus maniculatus	57	73.1	15	19.2	11	14.1
Peromyscus boylii	0	0	1	1.3	2	2.6
Neotoma cinerea	0	0	0	0	1	1.3
Microtus longicaudus	4	5.1	3	3.8	0	0
TOTALS	91	116.7	83	106.4	21	26.9
Trap nights	646		532		480	
Percentage catch	14.1		15.6		4.4	

*Third trapping after *Citellus beldingi* had entered hibernation.

The animals taken in the first period were chiefly inhabitants, but some may have "resided" outside of the area. Those of the second period were largely immigrants since the previous trapping; their numbers suggest the speed with which a small territory rendered vacant by elimination may "fill up." A 92 per cent "recovery" in population occurred although poisoned grain had been exposed nearby during this second period. The composition of the population was somewhat altered, since the larger species predominated in the reinvasion. In the third period there was a marked reduction in population; only 23 per cent as many were captured as in the first period. The weather was cold, with rain and some snow, and the lesser number may have been due to early hibernation by some species and to effects of the previous trapping and the poisoning. Nevertheless, the last trapping yielded a significant number of invaders, showing that repeated trapping will not eliminate rodents on a small area.

Further information on the rate of reinvasion was obtained near Carnelian Bay, at the north end of the Lake, where tests were made with snap traps to determine the number of rodents present on an area after poisoned grain had been distributed by state and county officials to reduce the hazard of plague infection. Trapping was first done soon after poison had been laid and again two months later. At the latter time, a nearby unpoisoned area, ecologically similar, was trapped as a control. The findings were as follows:

	July 21-23 (Soon after poisoning)	Sept. 21-24 (2.5 months after poison)	Sept. 20-24 (Unpoisoned control area)
Citellus beecheyi	0	1	1
Citellus lateralis	0	1	4
Eutamias amoenus	0	1	7
Eutamias quadrivittatus	0	9	5
Eutamias quadrimaculatus	0	1	12
Sciurus douglasii	3	0	3
Glaucomys sabrinus	0	1	1
Peromyscus maniculatus	0	3	10
TOTALS	3	17	43
Trap nights	48	129	172
Percentage catch	6.3	13.2	25.0

The July 21-23 trapping yielded no terrestrial rodents, but two months later the numbers taken on the same site were about half as many as found on the nearby unpoisoned land. Reinvasion was again evident, although at a slower rate than in Experiment 1.

Observations and additional tests were made to determine the effectiveness of poisoned grain in eliminating rodents. In an open spot, 3 miles south of Myers, having scattered conifers and many half-rotted logs, 50 small (B & B) live traps were set at 10-yard intervals on an area of 1.36 acres. All local rodents were marked, then poison was placed (Aug. 20-21), and shortly thereafter traps were again set and baited with oat groats at the exact stations previously used. Of the rodents then taken, the two chipmunks were individuals marked before poison was distributed, whereas the mice were "new" animals.

	August 5-16 (Before poisoning)	August 23-28 (After poisoning)
Eutamias amoenus	13	2
Eutamias quadrivittatus	8	0
Peromyscus maniculatus	19	1
Peromyscus boylii	0	2
TOTALS	40	5
Trap nights	550	300
Percentage catch	7.2	1.7

A similar experiment was tried at a garbage dump near Al Tahoe, using prunes and pine nuts for trap baits. The poisoned grain scattered there had not been accepted readily by rodents and there may have been an imperfect kill. The second trapping was made after a considerable interval and the extent of reinvasion could not be determined clearly.

	June 18-21 (Before poisoning)	August 24-27 (After poisoning)
Total rodents	102	27
Trap nights	308	180
Percentage catch	33.1	15.0

Watch was kept throughout the season for dead rodents and birds on areas that had been poisoned, and several small tracts were searched carefully. Just south of Myers one *Peromyscus maniculatus* and three Eutamias were found. Two field men spent an entire morning searching an area of about 20 acres that had been treated 2 to 5 days previously but saw only two dead Eutamias. During the entire season only two dead birds were found in poisoned areas—one Sierra junco at the Fish Hatchery near Tallac, and one spotted towhee at Rubicon Point. Both were in mummified condition and the causes of death could not be determined exactly; both species are ground-feeding seed eaters and may have been killed by poisoned grain. At Myers, a flock of 10 to 15 juncos that had been regular camp visitors disappeared at the time of poisoning operations and did not reappear during the two weeks following. The food habits of these birds are such that poisoned grain may have caused their disappearance, but it is also possible that they migrated out of the region or moved their feeding grounds to some nearby area not under our observation.

Conclusions from Tahoe Studies

1. Repeated trapping as a method of eliminating rodent populations is inefficient, as re-invasion usually takes place. If and when it is necessary to clean out rodents about mountain cabins on wild lands, more widespread and effective control measures are necessary.
2. The use of poisoned grain reduces the rodent population, evidently without conspicuous injury to other species, but is ineffective for small areas because of the subsequent quick reinvasion by rodents from adjacent non-poisoned areas.
3. Snap traps do not provide an accurate method of population census, because it is impossible to distinguish between resident and non-resident animals that are taken; also, it removes local individuals and thus allows the composition of the population to be altered by invasion of others. Snap traps, however, serve for a quick and less expensive estimate of population on an area that is to be poisoned and for a crude appraisal of the results of poisoning if used soon after the latter has been done.
4. Live trapping and marking of individuals is the best method now known for studying the composition of rodent populations.

BASS LAKE: 1938-1939

The conclusions from the Lake Tahoe studies provided a basis for the subsequent program at Bass Lake. The area chosen for study was in cut-over Transition Zone forest, 3.5 miles NNE of Bass Lake, at 4500 feet altitude, in the drainage of the North Fork of the San Joaquin River (Mariposa Quadrangle, U.S.G.S.). The soil there is a deep loam, the surface sloping (15 to 30 degrees) to the southwest, and the existing cover comprised many large logs and stumps besides living trees and some small vegetation (Fig. 3). The principal trees present were incense cedar, white fir, black oak, yellow pine, sugar pine, and white alder. Other plants included gooseberry *(Ribes roezlii)*, deerbrush *(Ceanothus integerrimus)*, lupines, and grasses (Bromus, Festuca, Agropyron, Danthonia). Some descriptive notes on this area have been published by Holdenried (1940).

FIG. 3. Bass Lake trapping area, general appearance.

Thirteen rodent species were caught or observed. Two species of deer mouse *(Peromyscus maniculatus* and *P. boylii)* were taken commonly throughout the trapping period, as were also the California ground squirrel *(Citellus beecheyi)* and the long-eared chipmunk *(Eutamias quadrimaculatus)*. Of less frequent occurrence were the chickaree *(Sciurus douglasii)*, gray squirrel *(Sciurus griseus)*, pocket gopher *(Thomomys bottae)*, pocket mouse *(Perognathus californicus)*, and meadow mouse *(Microtus longicaudus)*. The harvest mouse *(Reithrodontomys megalotis)* was taken three times, and the Tahoe chipmunk *(Eutamias quadrivittatus)*, mountain beaver *(Aplodontia rufa)*, and bushy-tailed wood rat *(Neotoma cinerea)* each once.

Methods

Two types of traps were used for mice or small chipmunks—the "B & B", about 2 x 2 x 6 inches, and another, 2 x 2 x 8 inches, designed during the study; both were made of sheet metal and had a swinging entrance door. The "Young" rat trap, of wire mesh and measuring 5 x 5 x 18 inches, with two sliding drop-doors, was large enough to capture squirrels, yet could be set so as to be sprung by small mice (Fig. 5A). The traps were placed in grid formation (Fig. 4), at intervals of 10 yards; the location of each was marked with a red stake, helpful especially when snow was on the ground and to respot the exact trapsites in the spring of 1939. It was necessary to build a shelter of bark or wood over each trap to protect captured animals from rain, hail, or snow and the heat of the summer sun. Cotton (later kapok) for bedding was always provided in the small sheet metal traps. Even with these precautions, animals in the latter often suffered from wet and cold. They experienced less discomfort in the wire mesh traps, although the latter were not stocked with bedding.

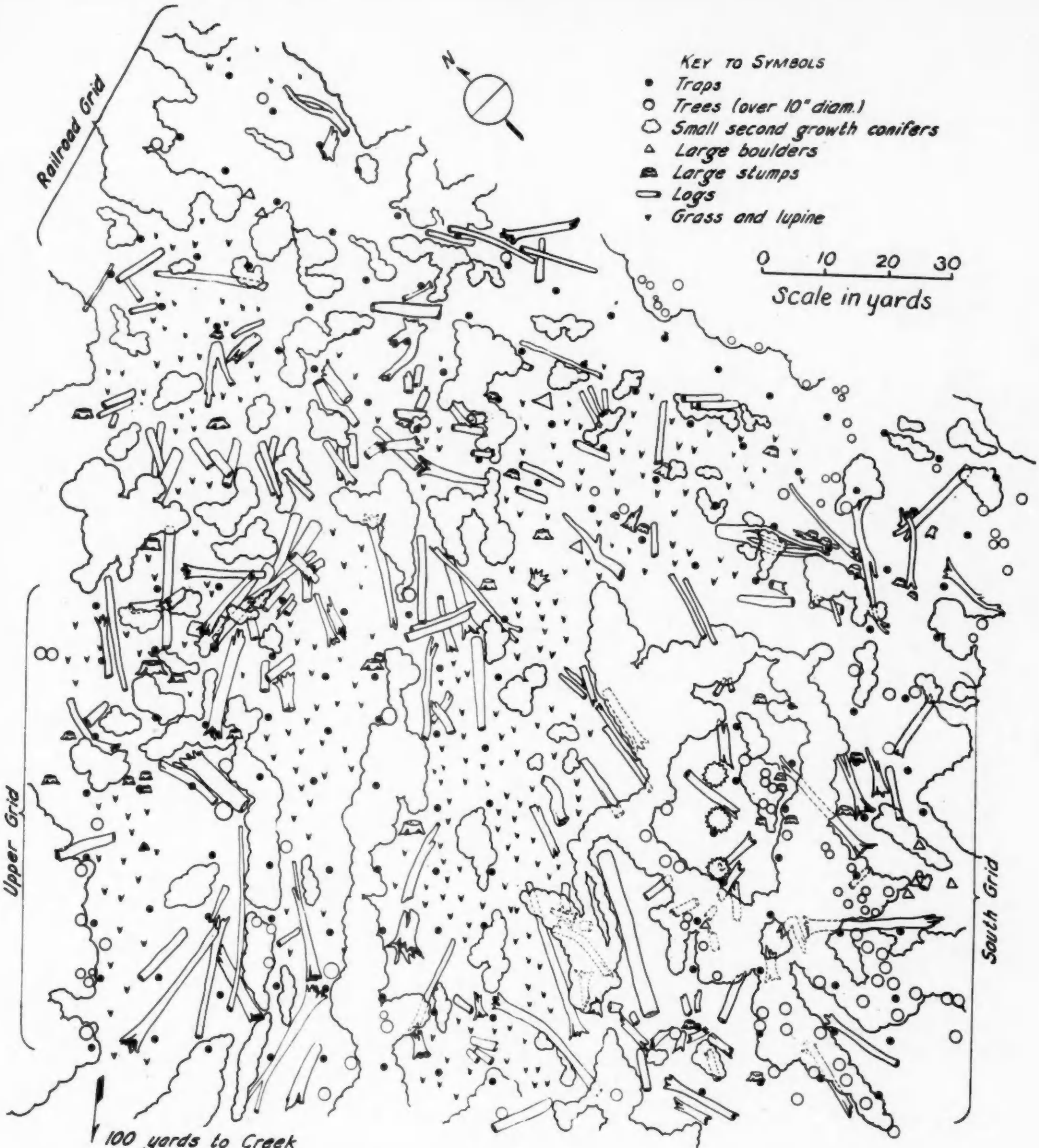

FIG. 4. Bass Lake trapping area, showing "grids" in relation to surrounding vegetation, logs, etc.

The several trap grids were run as follows: *Upper grid* (1 acre), with 64 traps, from July 6 to January 5 and from March 30 to July 8; *Railroad grid* (0.93 acre), with 32 traps from July 17 to September 17, and with 64 traps from September 17 to January 5 and from April 5 to July 8; *South grid* (0.39 acre), with 32 traps from August 17 to January 5 and from April 18 to July 8. On May 25 an encircling line of 54 traps was set 35 yards outside the grid boundaries, and on June 7 this was moved to 60 yards outside. The total number of trapping units was 23,653 trap nights and 26,771 trap days. During fair weather each trap was visited twice daily, otherwise but once; traps were closed and not attended on Sundays and a few other days.

Baits were not varied greatly during the field work. The "old-fashioned" type of rolled oats was the standard bait in the small metal traps. Pine nuts, sunflower seeds, raisins, and occasionally shelled peanuts were added at times for variety, but the rolled

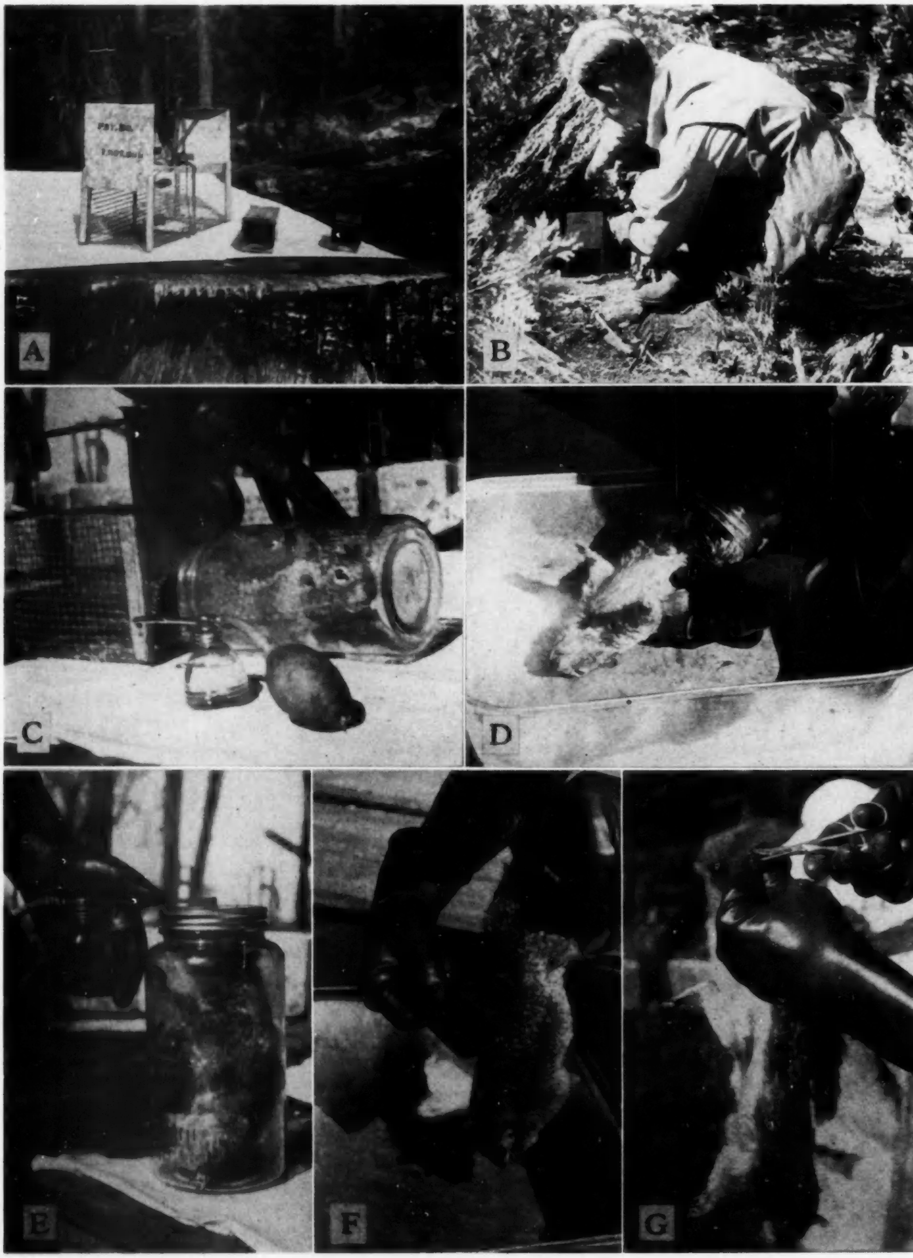

FIG. 5. Equipment and methods used in trapping and marking rodents and in removal of fleas at Bass Lake area. *A*. Types of trap used: "Young" trap at left, local model in center, B. & B. at right; all as set for use. *B*. "Young" trap being set beneath a stump. *C*. California ground squirrel passing from trap into jar for anesthesia. *D*. Anesthetized squirrel put into large pan. *E*. Chloroform vapor pumped by atomizer into jar containing squirrel. *F*. Combing fleas from squirrel. *G*. Marking squirrel, while anesthetized, by clipping terminal portion of toe.

oats appeared to be just as attractive as a mixed bait for most of the species. The larger Young traps were usually baited with whole dried prunes and rolled oats, often with the addition of pine nuts. A special type of hulled oats, known as "oat groats" and having the kernel only slightly crushed (used elsewhere to poison squirrels), proved successful with all rodents. In the fall, melon rinds and gooseberries were often tried as bait when many rodents were already feeding on these berries and other soft fruits, but these materials did not seem to make any appreciable difference in the catch. White fir cones, as cut by red squirrels, once were used successfully in the large traps to attract that species. Compressed pellets of "rabbit chow" were not attractive to the wild rodents, even in winter, but were not given any extensive trial.

The technique for anesthesia and removal of fleas developed in 1937 was used extensively (Fig. 5) and with much success. The amount of chloroform necessary varied with the size and species of animal; red squirrels seemed unduly sensitive and several died with but small dosages. A reduced dosage also was necessary with animals that were highly excited or had wet pelage and likewise with females advanced in pregnancy. After the removal of fleas, each rodent was weighed, measured, examined for signs of breeding, and marked if it was a new individual. In each species the individuals were marked by "toe clipping" (removal of terminal phalanx with scissors): FR 1 = inner digit of right front toe, etc. Not more than one toe on a foot was clipped, although some rodents had three toes marked. A ledger page was kept for each individual to record the site and date of subsequent captures, and for entries on breeding, molt, or other subjects. After examination, each animal was released at its place of capture. The records of rodents taken, as to species and individuals, were plotted graphically and compared with data on maximum and minimum temperatures for nearby weather stations, but no general correlation was seen between the two sets of data.

CHANGES IN POPULATION

The number of individuals trapped on the grids provided data for estimating the total active population per acre (Figs. 6 and 7). This varied from 19 per acre in late December to 60 per acre in July. The total active population during October was about one-half, and that of late December less than one-third, of the number in July. Small catches in the first few days of January, just before heavy winter snows, suggested that the population dropped even lower. Presumably the active individuals were fewest in mid-winter, but the lack of data then makes a definite statement impossible. A marked change with the seasons was evident. Numbers increased gradually in the spring and early summer to a peak in July, and thereafter declined steadily to the December low, by reason of death, emigration, and hiberna-

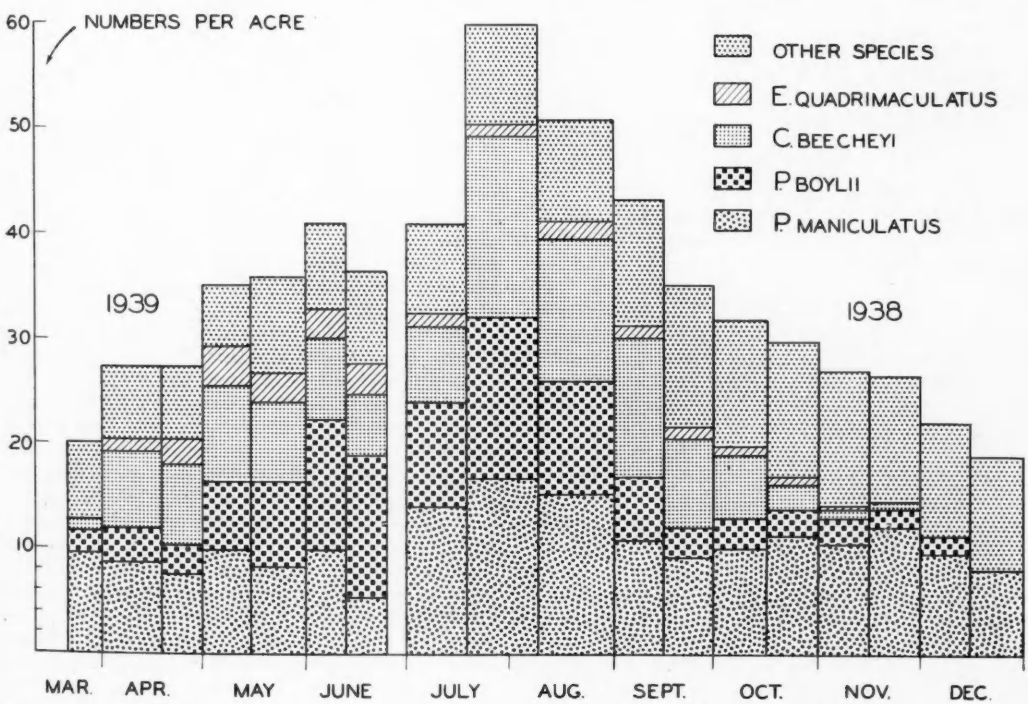

FIG. 6. Estimated total active rodent population per acre, by species, Bass Lake, 1938-39.

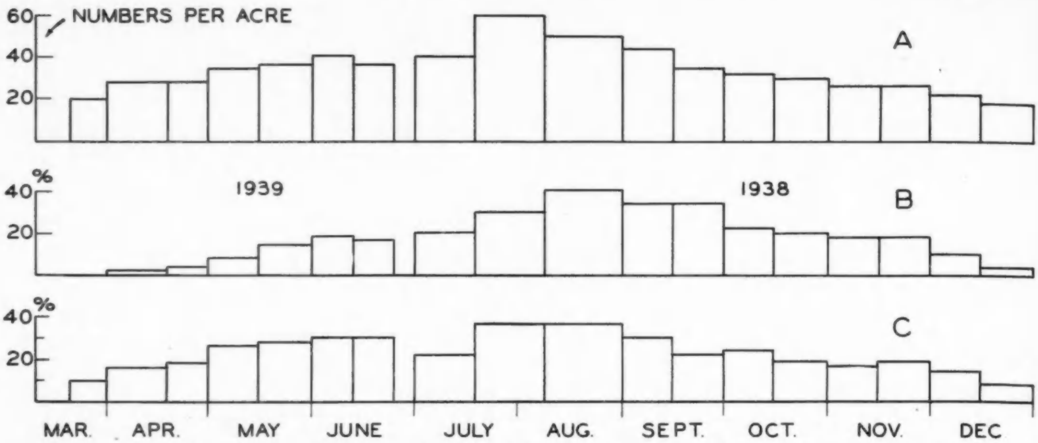

FIG. 7. Bass Lake rodents, all species. *A*. Estimated total active population, numbers per acre. *B*. Percentages of immatures. *C*. Percentages of non-residents.

tion. Thus the total active population of rodents pyramided about the middle of the calendar year; this may well be a general characteristic in local communities of small mammals.

The species composition of the population also was different at various times of the year. At the July peak, the bulk of the population was of *Citellus beecheyi, Peromyscus maniculatus,* and *P. boylii*. The decline in autumn resulted from the disappearance of *C. beecheyi, Eutamias quadrimaculatus,* and *P. boylii;* the first two went into hibernation by the end of October, and the latter apparently migrated away from the area mostly by the end of September. Several species of minor importance appeared in small numbers in the autumn and winter—*Perognathus californicus* from September 1 to December 1, and *Microtus longicaudus* from November to January. A few trapping records suggested that the local winter population was made up largely of *Peromyscus maniculatus* and *Thomomys bottae,* with possibly a few *Sciurus douglasii, Microtus longicaudus,* and *Peromyscus boylii.*

In still other respects, the total active population showed definite seasonal trends. This was evident in the percentages of immature and of non-resident rodents in the monthly records (Fig. 7). The midsummer increase in numbers was accompanied by greater percentages of these two groups in the total population. As the young matured the percentage of them naturally decreased; very few immature were present in December or in the following April. There was a similar shift, though less marked, in the percentage of non-resident individuals. In late December and again in March approximately 90 per cent of the population consisted of residents, but in midsummer the transients and non-residents comprised almost 40 per cent of the population. Despite these changes, immatures and non-residents were found during every month in which observations were made. Estimates of the active resident population gave a peak of about 39 per acre in July and a low of 17 both in December and March. The rise of the active resident population is evident from the following data: April, 23 per acre; May, 26 per acre; June, 29 per acre.

WEATHER AND FOOD SUPPLY

Seasonal changes in weather doubtless played an important part in determining the extent of activity. There was also a wide seasonal variation in the kinds of food afforded by the local vegetation. From January 5 to late March the area was covered deeply by snow, and the only green vegetation was on the conifers. Much of the area was still under 2 or 3 feet of packed snow when continuous trapping was resumed at the end of March. Part of the upper grid then was bare but had no fresh green vegetation, and such food as was present consisted of material on the ground exposed by the retreating snow. On March 31, when the first ground squirrels appeared, small blades of green grass were beginning to show; the gooseberry, deerbrush, and black oak then were starting to put out new leaves. By early May grasses and small lupines were abundant. The first plants to flower were dogwood, deerbrush, Sierra iris, lupines, western wallflower, and gooseberry. Probably the first fruits available were seeds of iris, wallflower and lupines, in rather small quantity. Green vegetation was abundant in early summer. In the late summer and early autumn fruits and seeds of grasses, lupines, and especially gooseberries were plentiful. Young ground squirrels were feeding on green leaves of lupines in the latter period. Later in September there were other foods; chipmunks then ate fruits of the dogwood and chickarees were harvesting the last of the white fir cones. A majority of the grasses then had dried up, but most of the lupines were still green; some of the gooseberries continued and a patch of thistles on the railroad grid bore ripening flower heads. The first freezing weather came on October

15 but did not last, and some vegetation remained fairly green into November. Early in that month there were still dogwood berries and large crops of elderberries; a few lupines bloomed until killed by frost about November 10. The black oaks then had a large crop of acorns, many of which dropped into the leaf litter under the trees. The early winter was fairly warm and mild, with a sparse growth of green grass, later buried by snow. The Peromyscus caught in February were fat and sleek, so must have had access to sufficient food.

Food Competition

There were seasonal aspects of competition in obtaining the food available. Cattle grazed freely on the grasses and lupines in the open areas from June to October, reducing the herbage and seeds available for rodents. A few deer were always present and foraged within the trap grids at night; in autumn they fed extensively on deerbrush, then practically the only green shrubbery present. Some birds which subsisted on the local seed crops were, in decreasing order of numbers, the Sierra junco, greentailed towhee, chipping sparrow, spotted towhee, and mountain quail. Several pairs of each of the first four species nested in the area, and individuals were often taken in the traps. Other birds which ate fruits and nuts in the trees were the black-headed grosbeak, blue-fronted jay, western tanager, western robin, band-tailed pigeon, and pine siskin. Early in November a flock of over 100 band-tailed pigeons fed for several days on acorns of the black oak. Pine siskins and goldfinches foraged on ripe heads of thistles.

Predation

Predation doubtless played its part in the changes that occurred in the rodent population, but actual evidence was scant. Weasels *(Mustela frenata)* probably were important. About July 10, 1938, a weasel was seen carrying a small rodent (gopher or meadow mouse?) in its mouth. Individual weasels, possibly some repeaters, were trapped on August 17, October 25, and November 5 and 10, 1938, and on May 11, 17, and 18, and June 24, 1939; they were usually released without handling. Several rodents were killed in the traps and partially eaten, probably by weasels; these included *Peromyscus boylii* on August 17, May 16, and June 24; *P. maniculatus* on May 18, and *Eutamias quadrimaculatus* on May 11. One pine marten *(Martes caurina)* was seen between the trapping area and Chilkoot Creek on August 17, as it ran rapidly down from the upper branches of a 25-foot white fir and bounded off through the woods toward the creek. Trappers reported that martens were abundant in the higher country. Three gray foxes *(Urocyon cinereoargenteus)* were seen on warm evenings in June down the road towards Bass Lake but none close to the trapping area. Tracks of foxes and skunks were often seen in the dusty road near the trapping area. Black bears were known to be fairly common in the region. Tracks of a large individual were seen along the old railroad bed on November 18, 1938, where it had occasionally nudged a trap out of place. About June 10, a trap was chewed almost to pieces by some animal, possibly a bear seeking a trapped rodent. Hunters in the area were known to have taken toll of the young ground squirrels in the autumn of 1938, and several young squirrels ended in the stew pot at a nearby woodcutter's camp. Raptorial birds were rather scarce. One red-tailed hawk was about for several days late in October, when some young ground squirrels disappeared. Cooper and sharp-shinned hawks were seen occasionally, and both horned and screech owls were heard after dark several times near trapping areas. Rattlesnakes *(Crotalus viridis)* appeared to be scarce in the forest; but two large individuals were killed on the road between Bass Lake and the trapping area on August 17 and May 1, respectively. A large rubber snake *(Charina bottae)* was caught in one of the traps on August 26, and another smaller one was taken by hand about June 8. A few small striped racers *(Coluber lateralis)* and Pacific garter snakes *(Thamnophis sirtalis)* were observed in open parts of the grids.

SPECIES ACCOUNTS

Peromyscus maniculatus

Season of activity. This species was active locally throughout the year and was apparently the dominant rodent in the area. Individuals were taken regularly in the autumn and winter up to and on January 5, when the first heavy snowfall ended trapping operations. The area was next visited for overnight trapping on February 23, and the traps, set on packed snow several feet deep, caught a male and a female *maniculatus*, both "repeats." The 19 traps set on March 23 on and about snow patches caught six individuals previously marked. During the rest of the year this species was always abundant. Trapping showed the mice to be entirely nocturnal; none was taken during the day that had not been released in the morning. In Maine, Johnson (1927: 276-284) found that some *maniculatus* entered traps in the daytime and concluded that this species is diurnal as well as nocturnal.

Breeding. When trapping began at the end of March, some of the females were in breeding condition, a few apparently were pregnant, and all of the males had enlarged testes. The first definite pregnancy was recorded on April 5, and the earliest record of lactation was in this same individual, on April 18; two other lactating females were taken during April. Of the 26 adult females taken in May, June, and the first week of July, all but one were pregnant or lactating at some time during that period. Pregnant and lactating females were also recorded from August to November, and there was one questionable record in December. Breeding apparently occurred locally from about mid-April to December, or from the time the winter snow pack melted in the spring until the heavy snows of the next winter arrived.

Throughout April all of the animals trapped were large old adults, many of which had been marked in

1938. The first juvenile individuals appeared in the traps on May 3 and 5; they were about one-half the bulk of adults. Ten of this size were taken during May; thenceforth such individuals were caught until January. There appeared to be two peaks in the population of young individuals, one in July and August and another in late October and November, with a sharp decline between (Fig. 8). Clark (1938: 233) stated: "The peak of reproductive activity occurs [in Peromyscus] from February to June, and then, after a brief lessening of breeding activity, litters often appear from mated pairs in August and September." The Bass Lake data indicated a lag of about two months in these peaks of reproductivity, especially of that in the spring; this might well be expected at the altitude of our trapping (4500 feet).

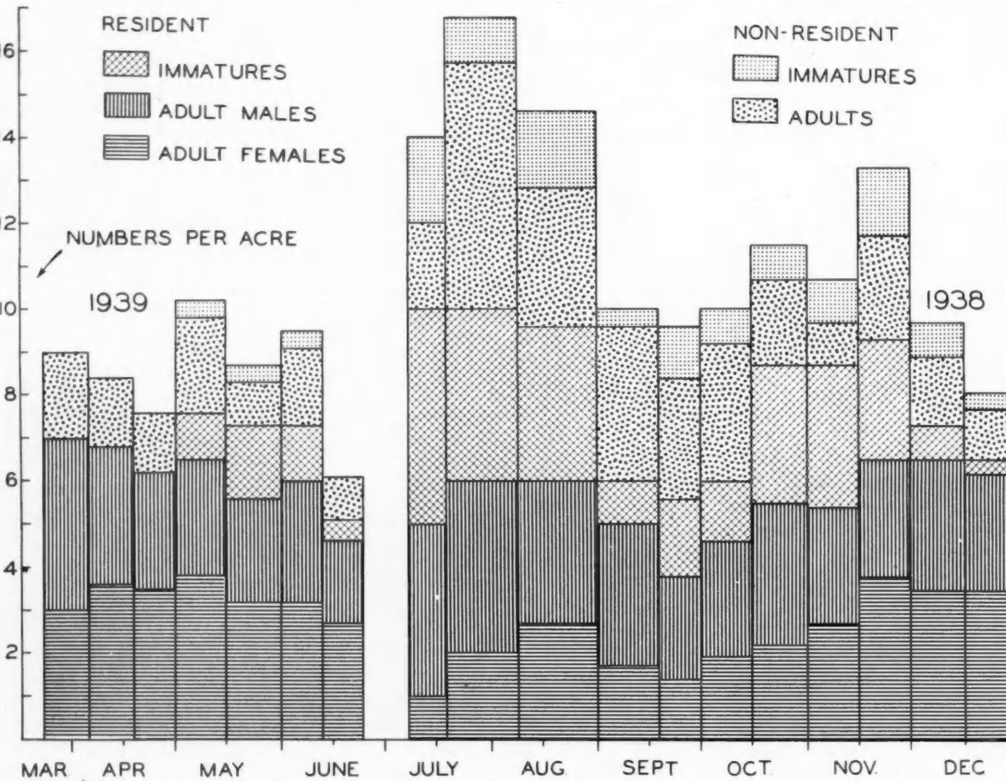

FIG. 8. Population of *Peromyscus maniculatus* at Bass Lake by age, sex and residence status.

Some of the females had new litters of young about every 30 days during the spring months (Fig. 9). The gestation period of this species is given by Svihla (1932: 31) as close to 23 days in non-lactating females and 25 days in those which are lactating, with a range from 22 to 35 [?] days.

Growth of young. The smallest individuals trapped were about one-half adult size and were in the juvenal blue-gray pelage; they were probably about one month old. Svihla (1935: 111) found that young of the sub-species *bairdii* were weaned at about 25 days and forced to shift for themselves as soon as a new litter appeared.

Young *maniculatus* undergo a post-juvenal molt when about six weeks old, according to observations on captive individuals by Collins (1918: 78-89), and Sumner (1917: 29). Change of pelage in the Bass Lake mice began to show laterally and progressed

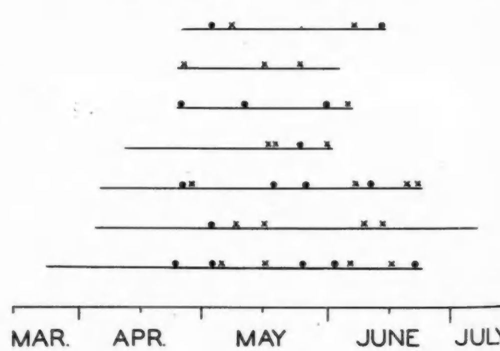

FIG. 9. *Peromyscus maniculatus.* Records of pregnancy (●) and lactation (x) in some individual females, showing production of successive broods through certain months at Bass Lake in 1939.

dorsally towards the head and tail; the last area to be invested was usually the dorsal part of the head, but in a few the molt on the head was completed before that on the rump. For convenience in this study, the post-juvenal molt was divided into ten arbitrary stages (Fig. 10). This saved much time in recording field data, as each molting individual could be placed quickly in one category or another without making freehand drawings.

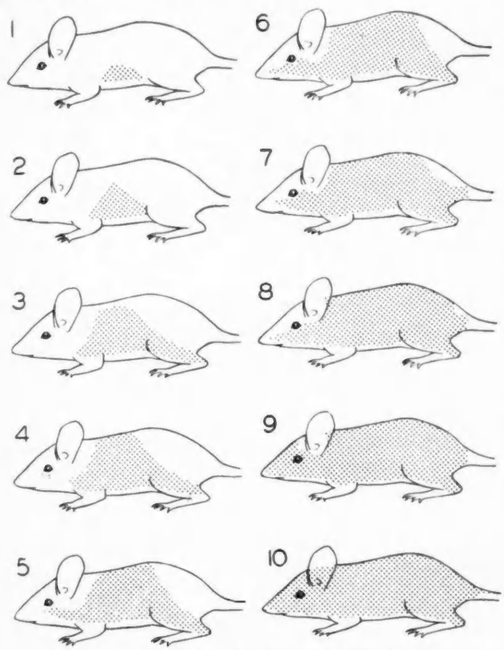

FIG. 10. Approximate stages in the progression of molt (stippled areas) in *Peromyscus maniculatus*.

The time required for completion of the different stages and of the entire molt varied with individuals (Fig. 11). After the first patch of new hair appeared on the sides the molt may be completed in as short a time as 8 days or require up to 35 days, averaging about 25 days. One individual did not molt for a period of 35 days, yet was nearly full-grown as to size; apparently it suffered from a mange-like condition, for its hair began to fall out in patches and it finally succumbed. The duration of the post-juvenal molt is given as about eight weeks by Collins (1918: 78-89), who described it thoroughly, and as about four weeks by Sumner (1917: 29). Collins points out that this molt may be well under way before it is noticeable on the surface; we did not search for new hairs within the blue coat and our data may not be entirely comparable with his.

Osgood (1909: 20) says, "In its early stages, this adolescent pelage is plainly distinguishable from the adult pelage." In field practice we found it almost impossible to distinguish between the post-juvenal and fully adult pelages. However, mice in post-juvenal pelage were usually smaller than full adults and were recorded as "young adults." Breeding records indicated that some females were sexually mature before they were fully grown; some individuals were pregnant before they had completed the post-juvenal molt. It seems probable that the young mice mature more rapidly during the summer when food is abundant and weather conditions are favorable. Clark (1938: 23) states that female Peromyscus may be sexually mature when only 34 days of age.

Home range and territoriality. Home ranges of individuals were determined by plotting on a map of the trap grids the points of capture for each individual caught more than five times; peripheral points were then connected by lines and the enclosed area measured. The results were as follows:

Peromyscus maniculatus	Number of cases	Home range (acres)		
		Average	Minimum	Maximum
Adult males	29	0.24	0.03	1.1
Adult females	27	0.21	0.01	0.66
Young males	10	0.13	0.01	0.24
Young females	12	0.12	0.02	0.31

Ranges varied greatly in size, but adult males appeared to have the largest, averaging slightly less than one quarter acre. A similar estimate had been made for *maniculatus* at Lake Tahoe. Young mice evidently had smaller ranges than adults.

The actual range of individuals may be larger than is here indicated, because the arbitrary drawing of lines on a map does not take into consideration differing topographic features, the possible wanderings of mice into areas where no traps were set, and the chance that individuals were not caught at the greatest limits of their ranges. We believe, however, that these figures give a fair approximation of home range.

The records of individual mice, plotted for each month, suggested that the home range of any single adult tended to be separate from those of other adults of the same sex. In about 90 per cent of the resident population, home ranges met but overlapped only slightly. Individuals of opposite sex evidently did not compete for territory, nor did the young mice, so that an adult male, an adult female, and several immatures might jointly have occupied parts or all of the same ground.

The boundaries of these home ranges were apparently rather elastic, varying from month to month, yet remaining fairly stable over long periods. Exclusive possession of a home range evidently could be maintained only by constant activity on the part of the inhabitant. Invasion seemed to occur chiefly when the owner happened to be in another part of his or her range. A home range made vacant by death or disappearance of an individual often was taken over by adjacent marked individuals of the same sex; less commonly, it was appropriated by unmarked mice from outside the trapping area. A few such unoccupied areas were acquired by marked juveniles as they matured. The overlapping which occurred occasionally may have been due to an abundance of food

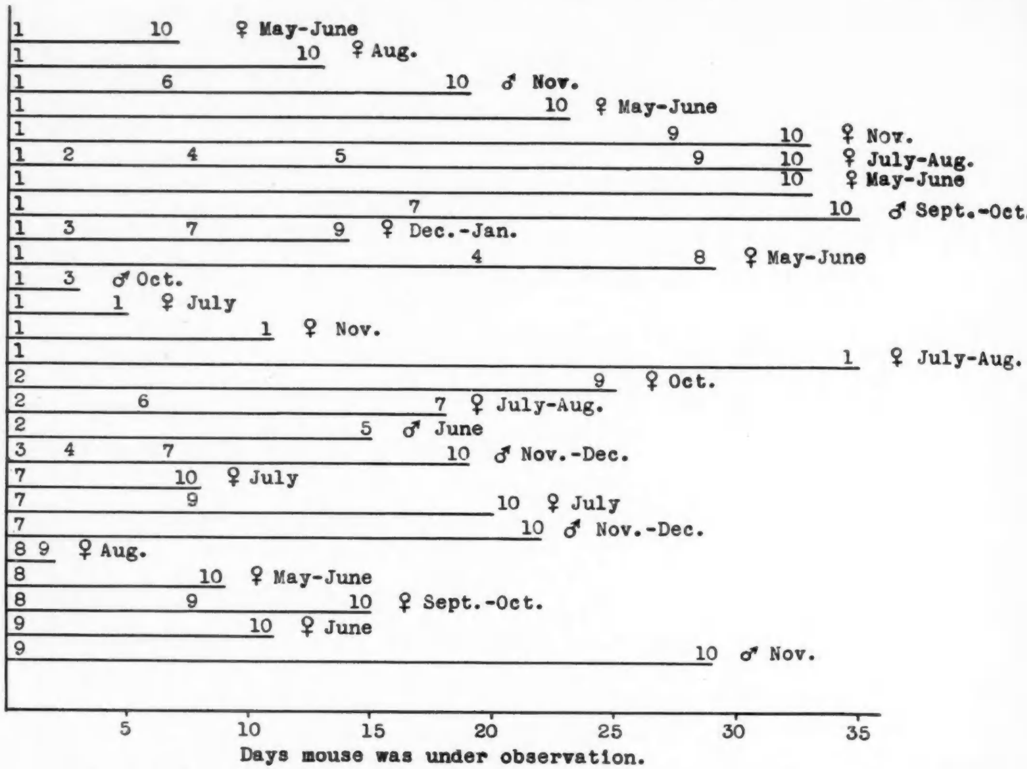

FIG. 11. Duration of post-juvenal molt in *Peromyscus maniculatus*. Length of line indicates extent of time in days between extreme observations on each individual; 1, 2 . . . 10, stages in molt as shown in Fig. 10. Sex and time of year during which molt occurred is given for each mouse.

and home sites in a small area, to a lack of pugnacity in the individuals concerned (perhaps a seasonal feature), or to equal matching of the mice in physical or other features. Transient mice or individuals living around the margins of the trap grid at times crowded over to feed at traps in territory already occupied by resident mice. Each example is recorded of an individual mouse (Fig. 12).

Local movements. A good deal of movement by individuals was recorded (Fig 12). We have interpreted our findings as indicating certain patterns in relation to residence, migration, and allied matters. In the illustrative examples which follow, the distances given are those between traps, and the distance from home range was measured between the farthest trap visited and the nearest trap in the periphery of the established home range.

1. Within the boundaries of the trap grids, quite a few of the resident population made short journeys away from their established home ranges, but returned shortly afterwards. This sort of movement was common among males during the breeding season.

Adult male: 29 captures in home range between July 8 and August 18; made a 60-yard trip south between August 12 and 16; returned August 17.

Adult male: 16 captures between July 19 and October 20; made a 53-yard trip from railroad to upper line on July 30; had returned home by August 9.

Adult male: 8 captures between October 26 and November 15; travelled 114 yards east to railroad line between October 26 and 27; had returned to home range by November 1.

Adult female: 4 captures between November 4 and January 4; taken in upper line 128 yards north of home range on November 18; had returned to home range by November 28.

2. The resident population exhibited a slow but constant shifting about; an individual would leave its established home range and take up a new one some distance away. This seemed to occur frequently in winter.

Adult male: 9 captures between November 27 and April 20; moved home range 75 yards east of original range between January 4 and April 6.

Adult male: 11 captures between November 3 and December 16; moved home range 155 yards from railroad to south grid between November 11 (when released on five inches of new snow) and November 29.

Adult female: 16 captures between October 21 and June 6; moved home range 50 yards west from railroad to upper grid between December 31 and April 25.

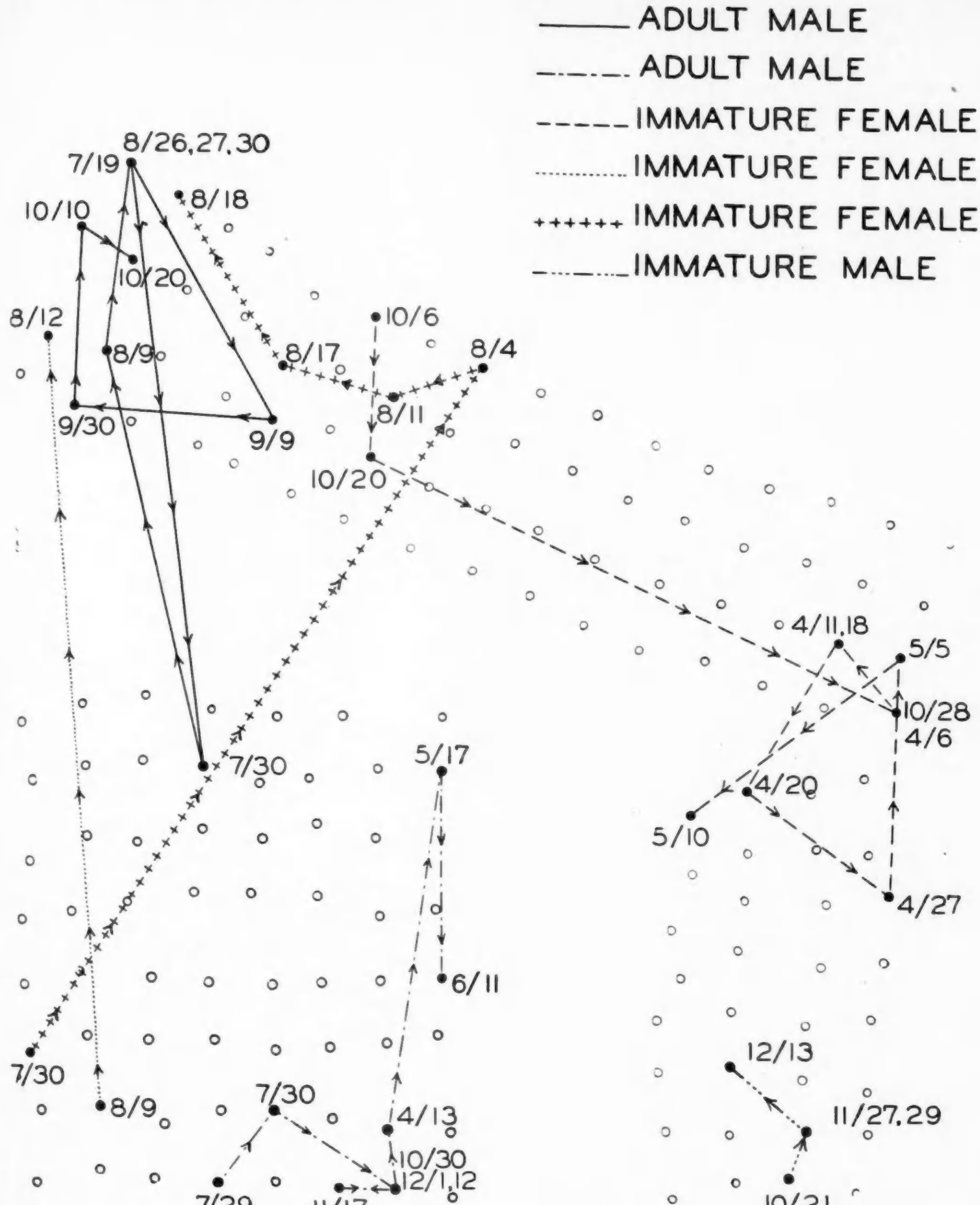

FIG. 12. Diagrams showing representative types of movement by various individuals of *Peromyscus maniculatus.* Dates of capture are indicated by month and day (8/26 = Aug. 26, etc.). Trap sites are shown as circles.

Adult female: 21 captures between October 28 and June 3; moved home range 45 yards from railroad to upper grid between April 14 and 19.

3. Unmarked adult individuals came from the outside, entered the trapping area, and established residence there.

Adult male: 10 captures between October 11 and May 3; appeared in area on October 11; next caught on April 11, 125 yards east, where home range was apparently established.

Adult female: 10 captures between December 1 and May 17; appeared in area on December 1; travelled overnight 90 yards east and established residence there.

4. Transient adults occasionally travelled through the trapping area for a few days.

Adult male: travelled 70 yards west across grid, July 28-30; disappeared (*i.e.*, not taken subsequently).

Adult female: travelled 63 yards east across grid, July 16-19; disappeared.

Adult female: travelled 94 yards north across grid, August 27-30; disappeared.

Subadult female: travelled 120 yards east across grid, August 9-12; disappeared.

5. Certain young mice born in the area or coming from the outside wandered about, apparently seeking homes.

Young male: ranged 97 yards along railroad trap line, June 9-24.

Young female: wandered 118 yards along railroad line, May 24-June 28.

Subadult female: 10 captures between October 6 and May 10; had moved 10 yards by October 20, and 90 yards by October 28; established home range and remained over winter.

Subadult female: 10 captures between November 18 and December 14; had moved 53 yards south by November 23; established residence there.

6. Mice living in marginal territory outside the trapping boundaries apparently came in to feed at peripheral traps.

Population changes. It was possible to distinguish two elements in the population: resident and non-resident. The resident population was determined by mapping the home ranges of individuals and was taken to include only those which ranged exclusively within the trapping boundaries.

The total resident population per acre (Fig. 8) varied from 5 in June to 10 in July and August, with an average of 7.6 for the entire trapping period. The adults of this group, with an approximately equal sex ratio, averaged about 5.8 per acre for the year, ranging from 3.8 in September to 7 in late March and early April. The immature population varied from none in the winter months to 5 per acre in July. The increase in the total resident population during July and August evidently was due to the greater numbers of young then produced. During September and the first half of October the records indicated a drop in the population, followed by a return to "normal" numbers late in October. This occurred among the young mice and to a lesser extent in the adults; it seems to have been chiefly the result of temporary cessation of breeding.

Non-residents were taken throughout the period of trapping, but were more abundant in the summer months. The total non-resident population per acre varied from 1 in June to 6.8 in July and August. The age composition of the non-resident population paralleled that of the resident group, with the largest numbers of young in early July and in November. Some mice evidently failed to secure home ranges when they matured, and competition for territory may well be continuous.

Changes in the total *maniculatus* population can be summarized thus: There was a noticeable increase in numbers during the summer months, because of increases in the numbers of young born and of transient individuals. There was a second peak of reproductive activity which yielded a smaller population increase in the late autumn. In the winter months breeding was apparently far reduced and population movements decreased, although activity did not stop altogether; as a result the total population was lower in the winter, but the seasonal change was less marked than that of other species in the area.

Peromyscus boylii

Season of activity. Peromyscus boylii was less common at Bass Lake than *P. maniculatus* and appeared to have a more definite season of activity. Numbers were low in the spring and autumn; none was taken in the latter half of December. A marked adult male was caught on February 24, and a few individuals were probably present throughout the winter. The season of greatest activity, as indicated by the number of individuals and by the percentage catch of the traps, appeared to be from June through August; then there were about as many *boylii* as *maniculatus*. The rapidity with which *boylii* increased in the spring and declined in the autumn suggested that both activity and breeding were responsible. Like *maniculatus*, this species seemed to be strictly nocturnal. Individuals were never caught during the day, except when they had been released in the morning. One or two were taken just after dark.

Breeding. The first pregnancy in *boylii* was recorded on April 7, and the first lactation on April 18. Breeding evidently took place as early as March. In 1939, pregnancy and lactation increased through the spring months to a peak in June, and dropped off gradually in July. Data from 1938 indicated that this decrease continued through the succeeding months, and there was no evidence of pregnancy or lactation after September. Immatures were taken in greatest numbers during June, but none was caught in the resident population after August, except for a few in December (Fig. 13). Thus *boylii*, unlike *maniculatus*, did not show a second peak in reproductive activity in the early fall. By October the testes of some adult males were far reduced in size.

No statement as to the length of the gestation period for this species has been found. Some of our field records suggest the number of days between litters as follows: 27, 25, 28-31, 25-27, 27-29, 31. It is likely that the gestation time in *boylii* is similar to that in *maniculatus*.

One female gave birth to three young in a trap on July 11. Another on June 20 gave birth to one but died in chloroforming; dissection revealed two additional embryos in the uterus. A third female, which died under chloroform on May 10, had recently given birth to four young, as indicated by placental scars. These young mice examined at birth were about 30 mm. in crown-rump length, pink and wrinkled, apparently naked except for the vibrissae, with closed

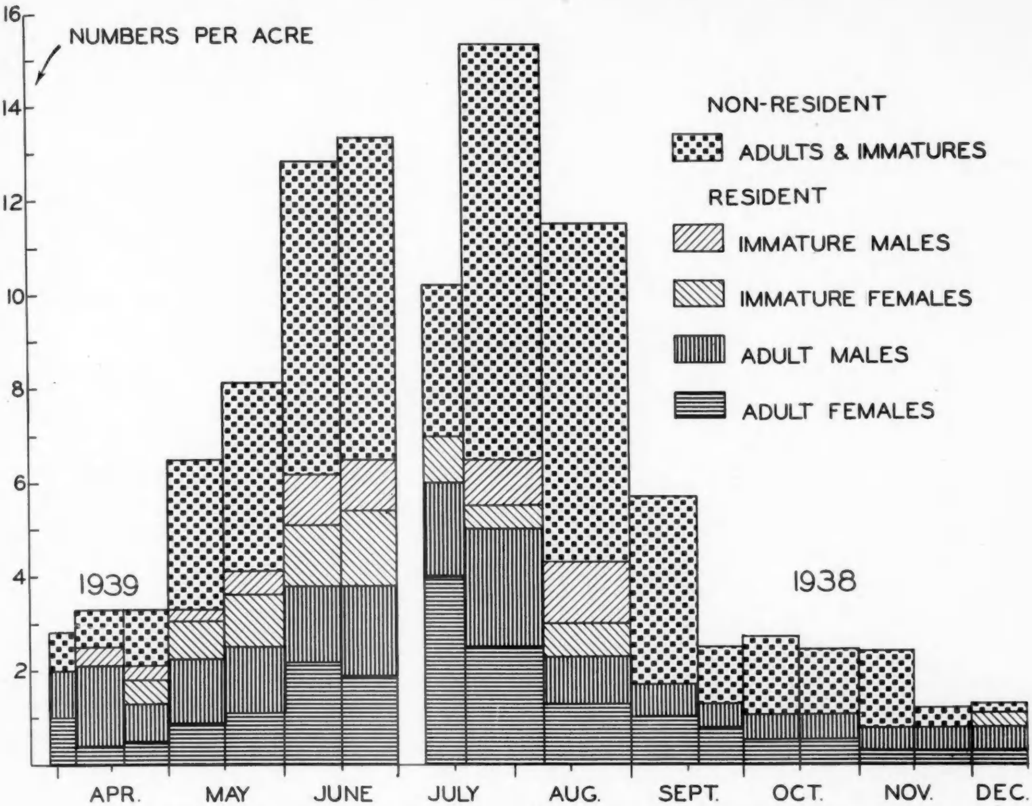

FIG. 13. Population of *Peromyscus boylii* at Bass Lake by age, sex and residence status.

eyes, and the pinna of the ears folded down as in other species of *Peromyscus* (Svihla, 1932: 23).

Growth of young. The first young in blue-gray pelage were taken on April 11 (when about half-grown), and the first molting immature (subadult) on April 18. It seems probable that young individuals may remain in the parent nest even after birth of a second litter, as females just beginning lactation were commonly taken in the same trap with small, gray-pelaged juveniles, presumably of a previous litter.

The youngest individuals were about one-third adult size when they first appeared in the traps. A few were so small as to be mistaken for half-grown *maniculatus*. Young *boylii* also had a post-juvenal molt (Fig. 14), the development of which was very similar to that in *maniculatus*. Young female *boylii* apparently matured more slowly, since few gave any indication of pregnancy until some time after completion of the post-juvenal molt. A few young males, however, had enlarged testes before their molt was completed.

Home range and territorialism. The home range of *boylii* appeared to be larger than that of *maniculatus*, but proved much more difficult to measure because *boylii* was more prone to wander and evidenced migratory behavior. The home range was not determined for any immature *boylii* and only for a limited number of adults, as follows:

	Number of cases	*Home range (acres)*		
		average	*minimum*	*maximum*
Adult males	13	0.27	0.04	0.95
Adult females	15	0.41	0.06	1.6

Unlike *maniculatus*, the adult females seemed to have larger ranges than adult males.

Individual territories were not so evident with *boylii* as with *maniculatus*, but the same kinds of territorial relations were observed among resident adults as in the latter species. The apparent separation of ranges may be a spacing out of individuals to insure a sufficient food supply for each. Many *boylii* whose normal ranges were outside the boundaries of the trap grid visited peripheral traps, apparently to feed, and in so doing overlapped the home ranges of resident mice.

Local movements. The records for *boylii* showed all the patterns of local migratory behavior observed in *maniculatus*, but certain types (Nos. 2 and 3) appeared to be particularly prevalent. Most significant was a noticeable seasonal migration to and from the trapping area. Of 51 individuals marked in 1938, only one (an old, one-eyed female) was recap-

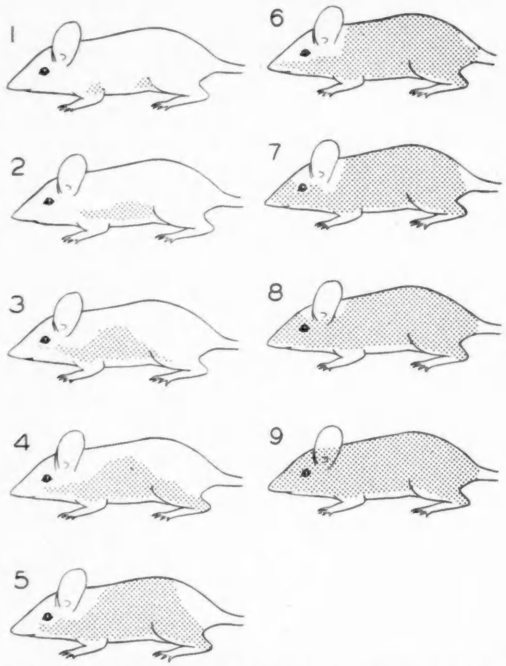

FIG. 14. Approximate stages in the progression of molt (stippled areas) in *Peromyscus boylii.*

tured in 1939, although many unmarked old adults then were taken. Several of those taken in the upper grid during March and April later established residence in the south grid after the snow had melted there; it seems probable that they were migrating into the area when first caught. These movements were most noticeable in the spring and again in the early autumn, when the population showed a definite decrease. The trapping statistics for *boylii* superficially resembled those for *Citellus beecheyi* which hibernated in this area; so far as known, however, no Peromyscus hibernates. It is possible that *boylii*, being semi-arboreal, may find more food in the nearby heavily-wooded areas and may cease foraging on the ground in open places when available food supplies there are low.

Population changes. The distinction between resident and non-resident groups was more definite in *boylii* than in *maniculatus* (Fig. 13). The total resident population per acre ranged from 0.8 in November to 7 in June; there was a rather abrupt decrease in September to the low figures of winter and a fairly rapid rise in the spring to the summer peak. No *boylii* was taken in late December when *maniculatus* still was active. The resident adults (with females slightly more abundant than males during most of the year) varied from 0.8 per acre in December to 6 in July, and immature residents varied from 0.4 per area in April to 2.7 in June. The resident population of immatures probably was higher than our figures indicate. During the height of the breeding season the resident immatures averaged between 1 and 1.5 per breeding female, a rather low figure considering that some females had several litters in the spring and early summer. The practice of classing young individuals as adults when they had completed the post-juvenal molt may account for some of this discrepancy. It is also likely that many immatures migrated to outside territory not long after they left the parent nests and therefore were not included as residents.

The non-resident population per acre varied from 0.2 in December to 8.3 in July. The trend was very similar to that of the residents. The non-resident population equalled or exceeded the resident population during much of the trapping period. In the first half of September the non-residents made up 70 per cent of the total population. The difference between *boylii* and *maniculatus* in this respect was marked, for the non-resident group in the latter never attained to more than 42 per cent of the total population.

The total *boylii* population can be summed up as follows: With a marked season of activity, evidence of migratory behavior, and a large non-resident element, the population displayed a clear seasonal trend, ranging from low numbers in the winter to a peak in July and August. The increase was due partly to a greater number of immature residents, but from May to November the population comprised at least 50 per cent non-residents. The total population was influenced much more by migratory activity than was the case with *maniculatus.*

Eutamias quadrimaculatus

Season of activity. Available records indicate that this chipmunk was active locally from late March to about mid-November. The first chipmunk of the season (probably this species, but possibly *E. merriami*) was seen at about 3,800 feet altitude on March 17, a warm sunny day. Continuous trapping on the area began on March 22, but no chipmunk was taken until April 7; all this time snow lay thickly in places.

In the autumn of 1938, no adult was taken after October 25, although a few immatures remained out as late as November 4; the first "cold spell" occurred from November 10 to 14; about six inches of snow fell and the temperature dropped to 14° F. at night. Most of the chipmunks active in the autumn were immatures; a majority of the adults evidently were inactive or in hibernation by November 1. Whether they resumed activity during favorable winter weather could not be determined. We neither saw nor heard chipmunks from November 4 to January 5, when winter really set in with heavy snow, but they might then well go unnoticed unless "chipping"; they were seen rarely even when very active. Records for the Yosemite region (Grinnell and Storer, 1924: 189), indicate that in 1914 this species was active at Chinquapin (6,200 feet) as late as November 26, but apparently all had hibernated there by December 30.

Breeding. All of the males, when first taken in April, had greatly enlarged testes. During late April

and early May, males were active in pursuit of females; on several occasions a male and a female were taken together in single traps. Some females so caught were in breeding condition, as evidenced by the appearance of the vulva and their subsequent history of pregnancy and lactation; others seemingly did not breed until later. One female began to lactate on or about May 31; another did not do so until July 22, 53 days later, but may have lost an earlier litter. Nine females caught between June 1 and 23 were apparently in early stages of lactation. Lactation apparently may continue for 35 or 40 days, possibly longer.

Our meagre records seem to bear out the report by Ross (1930: 77-8), from observation of captive individuals, that the gestation period is about 31 days. Most of the breeding evidently took place in the first two weeks of May, and the majority of young were born between June 1 and 14.

Growth. The first young taken in 1938 were a male and female found on July 8, crawling about under a small white fir. Our attention was attracted by their constant squeaking; both were covered with ants and fleas, and their eyes were not fully open. Their bodies were about the size of an adult *Peromyscus maniculatus*, but the head, legs and tail were proportionately larger; the hair was very short and silky and the skin appeared quite black. The female died two days later, but the male was raised successfully and kept until October 15, when he was fully grown and indistinguishable from an adult. His disposition was such that only one person could handle him without being bitten.

One immature male about two-thirds adult size was caught on August 2, 1938. This was probably the time at which most of the young emerged. No other was taken until the first part of September when the young were almost fully grown. In 1939 the first immatures were taken on July 26 and 27, and probably were from early litters.

Home range and territoriality. The following figures suggest the size of home ranges in this chipmunk:

	Number of cases	*Home range (acres) average*	*minimum*	*maximum*
Adult males	13	2.2	0.8	4.6
Adult females	8	1.2	0.8	1.6

Males evidently ranged more widely than females. These records were obtained largely in the spring of 1939 during the breeding season, and the home range may be different at other times of the year. The observed range was rather large, considering the size of the animals; this may result from the active nature of *quadrimaculatus*. Some individuals had larger ranges than any recorded by us for *Citellus beecheyi*, a much larger species.

At all seasons, but especially during breeding time, the ranges of individual male chipmunks overlapped extensively, with little sign of exclusive territorial possession. That this was not without protest by certain individuals may be inferred from evidence of fighting among the males; in the breeding season almost every male had cuts, especially about the face. Female chipmunks apparently maintained separate ranges for the most part, with slight overlapping of boundaries. If territory is held by individual females, it is probably maintained only by constant defensive activities as suggested by Gordon (1936: 171-2; 1938: 78-84), who concluded that there was an order of social dominance among chipmunks and some other sciurids, based on the ability of an individual to defend itself and its territory.

Local movements. Little was learned of the migratory activity of these chipmunks, because of their larger home ranges and the limited area covered by traps, together with the infrequency of capture (Fig. 15). Several individual males repeating from 1938 were caught between April 7 and 19, 1939, and 14 unmarked males were first taken between April 25 and 28. The reason for this sudden influx of males was not evident. It is unlikely that they were just emerging from hibernation. Perhaps there was a dispersal of males in search of mates before the breeding season proper began. With two exceptions, these new males took up residence in the area. Most of our marked individuals were trapped in the same small area in autumn and spring, but some individuals possibly migrated to warmer places at lower altitudes in the fall.

Population changes. There was little indication of a non-resident element in the chipmunk population, hence all were treated as residents. The population per acre was computed for the area within the encircling trap line (approximately 11 acres) rather than for the smaller area of the trap grids.

The active population of this species increased rapidly in the spring and early summer, as individuals emerged from hibernation; from 0.5 per acre in April it attained a peak of 2.5 per acre in June. There was a definite decrease in July; no chipmunks were trapped in August, although several then were active in the area. This change may have been due to the observed preference then for ripening gooseberries over the dry rolled oats, pine nuts, and prunes with which the traps were baited. Gooseberries used as bait were rarely successful, apparently lacking the "appeal" of fresh fruits on the bushes. The active population decreased in autumn as individuals went into hibernation or possibly left the area. The number of individuals per acre dropped from 0.5 in September to 0.1 in early November. A more detailed study of this species in the same area from August through November, 1939 (Holdenried, 1940: 405-411) indicated a similar trend.

During April, 18 males and 2 females were caught. It is probable that males emerged from hibernation earlier than females. A similar tendency was observed by Schooley (1934: 195) for the chipmunk, *Tamias striatus*, in Indiana. The population of females, as indicated by our trapping, increased slowly during the spring. Most of them apparently were out by May 15, but unmarked individuals continued to be caught until June 15. All of the females trapped in June were lactating, indicating that they had been

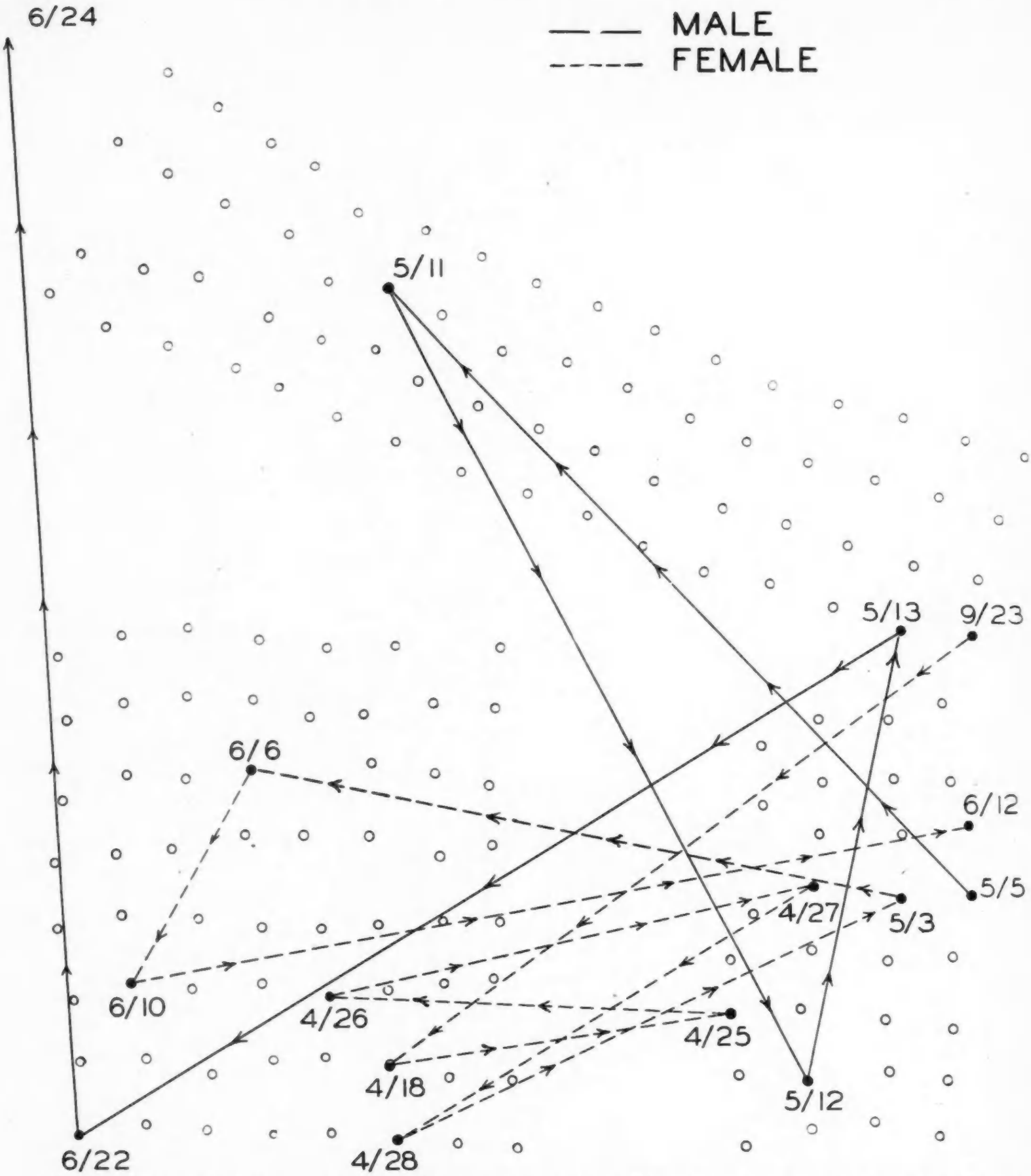

FIG. 15. The movements of two adult individuals of *Eutamias quadrimaculatus* as revealed by successive captures; ———, ♂ FR2-FL4,-----, ♀ FL2. Compare Figs. 3, 12, and 17.

out for at least one month. Immatures made up the bulk of the autumn population, as adults apparently went into hibernation before the young.

Citellus beecheyi

Season of activity. The period of activity above ground evidently extended from about April 1 to November 1. The first squirrels on the trapping areas were seen on March 31, when most of the snow had melted from open parts of the grid but extensive patches remained in shaded spots. At a lower altitude (3,500 feet) near Bass Lake, one was seen on February 27; and in mid-March, even on cold, misty days, a number were active there, with signs of early breeding. In the trapping area, most of the squirrels apparently had emerged from hibernation by April 12, as 11 of the 12 resident females and 2 of the 5 resident males had been taken by that date. Females

evidently emerged shortly before the males. The squirrels were active throughout April, when old burrows were cleaned out and new ones dug.

Females apparently went into hibernation before the males, since only 2 females were caught after September 25 and at least 7 males were active in mid-October. This agrees with data published by McCoy (1912: 1070) and with observations of *C. b. douglasii* in central western Oregon by Edge (1931: 195), who suggests that the difference may be "caused by the necessity of the female to provide for the young in the spring. The continuing of this food gathering habit after weaning results in an accumulation of fat earlier in the fall." Females were recorded by us as "fat" by August 2, 1938. Of 12 females marked in 1938 and recaptured in 1939, all had disappeared by September 23, 1938. Most of the adult males of 1938 had much loose, baggy skin when last caught in the autumn. The last date of capture for an adult male was November 26.

The young of the year were very active in September and early October, but only one male and three females remained abroad after October 15; two of these females were last seen on November 10 and 26, respectively, and the former was the first individual to be caught the following spring.

Breeding. Breeding apparently occurred in the latter part of April. The testes of all males taken in April were much swollen, but were reduced by late May. During April and May the females increased rapidly in weight (Fig. 16) and only one of 20 females did not then appear to be carrying young.

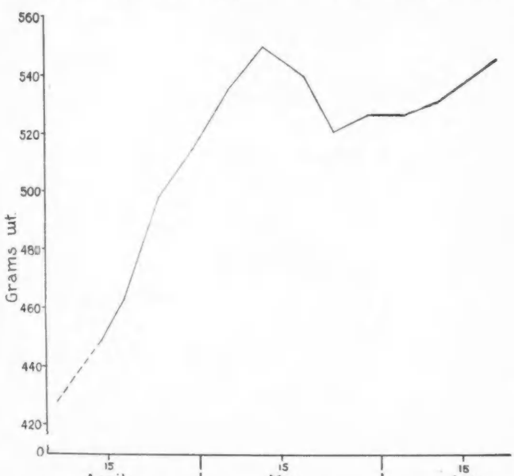

FIG. 16. Average weights of adult females of *Citellus beecheyi*, combined from records of individuals, known yearlings being excluded.

Pregnancies were observed from May 18 to June 1, and lactation from May 25 to June 9. In 1939 most of the young evidently were born between May 20 and June 1, but a few litters may have been produced later. There was only one litter per mother per year.

Growth. In 1938 young squirrels were not observed until late July. The first juvenile, a male about the size of a large chipmunk, was found injured, dragging its hind legs, on July 18. No young were trapped until July 28, and but few were caught until early August. When first taken they were only slightly larger than big chipmunks, or about one-fourth the size of the parent squirrels. No weights were taken in the early part of this season, but the young grew rapidly and were quite fat by October, when many of them weighed over 400 grams. In 1939 breeding evidently was earlier than in 1938, because the first young were seen above ground on July 7 and 8; at that time, according to breeding data, they were about 7 weeks old. Thirteen young caught on those days averaged 194 grams in weight, or considerably more than the 65 grams given by Edge (1931: 197-198) for young *douglasii* of about the same age.

The loss of weight during hibernation may be quite considerable. A young female weighing 400 grams when last caught on November 10 was down to 236 grams when next caught on March 31; a second immature female weighed 450 grams when last caught on November 26, and 286 grams when next taken on April 11. These losses represented 41 and 37 per cent, respectively, of the total body weight. Comparable data for adult squirrels were not obtained because of limitations in equipment for weighing. Before going into hibernation, most of the adults weighed more than the maximum of 650 grams recordable by our scales. In the following spring 20 adult females averaged 469 (272-648) grams at first capture, and in April the adult males averaged over 600 grams.

Home range and territoriality. The home ranges, determined by the same methods used for previous species, were as follows:

	Number of cases	*Home range (acres)* *average*	*minimum*	*maximum*
Adult males	9	0.85	0.26	1.3
Adult females	20	0.64	0.12	1.7
Young males	7	0.41	0.15	0.7
Young females	13	0.53	0.12	1.3

Adult males evidently had the largest average home ranges, and those of adults were larger than the ranges of immatures. These ranges were spaced out to a certain extent, due perhaps to competition for food and for burrow sites, but there was little evidence of exclusive territories since the ranges of some individuals overlapped widely at all times.

Local movements. The movements of individuals could not be followed if they disappeared from the trap grids, because of the rather small extent of the trapping area. Some individuals showed a shift of several hundred feet in home range from 1938 to 1939, but the majority of the resident squirrels remained in much the same area from the one year to the next. During the breeding season in April and May, both males and females wandered about extensively (Fig. 17). Eleven males and 9 females

were captured only once or twice and then disappeared. In the autumn before hibernation, and especially in September, many of the young disappeared from the trapping area, probably dispersing to search for new homes. Of 52 young marked and released in 1938, only 6 (11.5%) were retrapped in 1939. In contrast, of 29 adults marked and released in 1938, 16 (55%) were recaptured the following year. The greater decrease of young was probably due in part to various factors; they are more susceptible to disease, more easily captured by predators, and less well prepared to withstand winter hibernation.

Population changes. On the relatively small area we used it was difficult to determine which individuals were residents; only those which seemed to spend most of their time inside the boundaries of the grids were so considered. In 1939 the resident adults probably comprised 14 females and 6 males, of which 4 females were marked as young in 1938 (Fig. 18). In July, August and September, 1938, the marked young of the year totalled 13 females and 9 males. Possibly more young males were driven out of the desirable territory. Only one male marked when young in 1938 was recaptured in 1939, and then only once and in marginal territory.

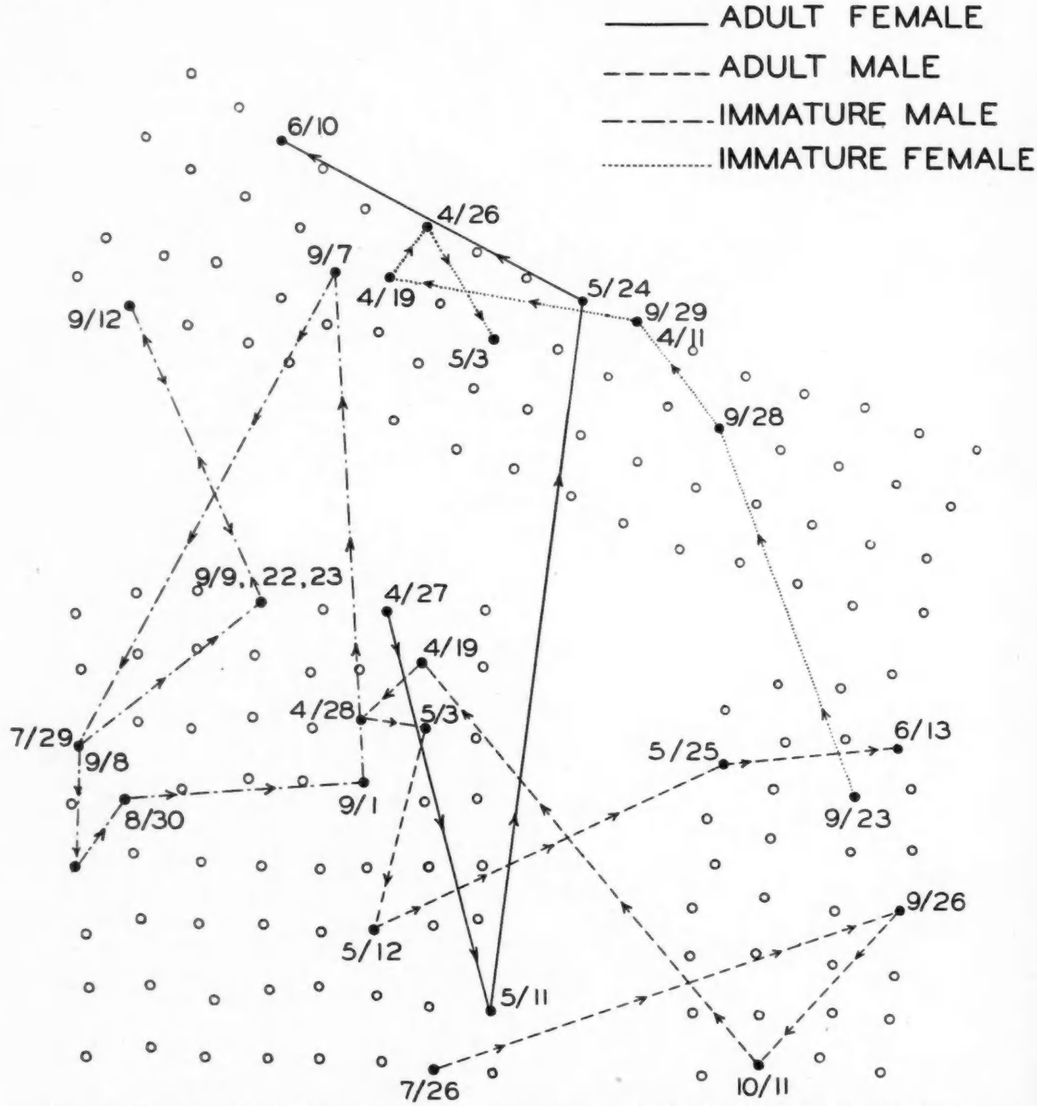

FIG. 17. Diagrams showing representative types of movements by individuals of *Citellus beecheyi*: ———, adult ♀ FR4-HR2; -----, adult ♂ HL2; ...., young ♀ FL2-HR3; — - — -, young ♂ HL5. Compare Figures 3, 12, and 15.

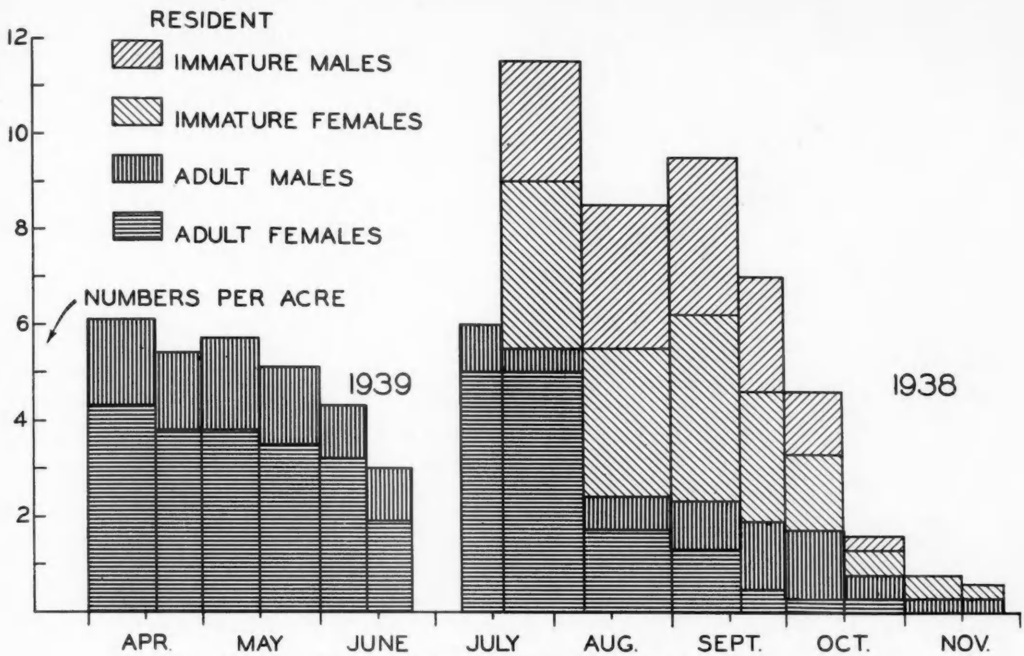

FIG. 18. Active resident population of *Citellus beecheyi*, per acre, by sex and age.

The population per acre ranged from about 7 in April to 17 in July, and decreased rapidly thereafter with the coming of autumn and hibernation. Like the chipmunks, the ground squirrel population displayed a marked seasonal trend and was subject to greater annual differences than appeared in less seasonal species.

Thomomys bottae

Seventeen pocket gophers were taken in our traps, from one to twenty times each. This suggests that in mountain areas gophers are more active on the surface of the ground than has been supposed. Their above-ground activity occurred largely during the night or early morning, although a few captures, particularly of young, were made in the daytime. Fifty of the 72 captures were made in November and December. The first cold weather and snows probably brought these rodents to the surface and they continued active on or near the surface of the ground during the winter. "Snow plugs" were in evidence everywhere on the trapping area after the snow had melted off in the spring. Winter activity of gophers and snow tunnels in the Yosemite region have been described by Grinnell and Storer (1924: 139-140).

Two adult males taken on April 20 and 21 had the testes much enlarged; an adult female recaptured eight times between April 6 and 22, however, showed no signs of breeding. An adult female was lactating on June 21 and also on July 25 to 27, suggesting either a long lactation period or the birth of two litters in close succession. The earliest young was a female taken June 21, 22 and 23; she was about one-third adult size and probably just out of the nest. Two juveniles about two-thirds grown were taken on July 21 and August 24, respectively, and two others, half-grown, on November 10 and 22. A long breeding season is indicated. Adult males in late November and December had small testes, and adult females then showed no evidence of breeding.

Records of color aberrations in the pocket gophers are uncommon enough (Storer and Gregory, 1934; 300-312) to warrant mentioning a melanistic adult male taken on April 21. It was shiny black above, light grayish buff on the under parts, feet, and tail, and the vibrissae were white.

Several gophers dug lateral runways from their main burrows to emerge directly under the bait pan of certain traps. The bait was frequently dislodged and shaken down into the burrows. Gophers relished rolled oats and dried prunes. When one was caught it usually consumed all of the bait in a trap. Green food was scarce when most of the adults were taken in November, December, and April, and it may be that much of their natural food in those times is of seeds and dried wild fruits.

Wherever a gopher was trapped, there was usually an open burrow close by. Some individuals would, upon release, go almost directly to such burrows, although a few attempted to escape by digging. Twice an old female went almost directly to burrows 25 and 40 feet distant, respectively, from the trap. One male was taken several times up to 30 yards

away from his usual point of capture. The only evidence of migration was furnished by an immature male taken in two traps 84 yards apart between November 10 and 12.

The number of gophers caught indicated a population of 4.6 per acre, but the actual population more probably was at least twice that figure. During the autumn and winter months, adult females were taken more frequently than adult males; the reverse was true in the spring, when the males presumably were seeking mates.

Perognathus californicus

The presence of pocket mice on the trapping area was not known until September 1, when a subadult male was taken. Between that date and December 1, twelve individuals were trapped; one other, a male with large testes, was taken on May 27. Pocket mice were probably present during the remainder of the year, but went uncaptured because of unsuitable baits or trap sites. These mice showed a marked habitat preference. Almost all were taken in open and partly bare areas of sparse grass, low lupine, gooseberry, and scattered small incense cedars; none was caught in the timbered part of the trap lines. Males taken in the late autumn and winter had small, retracted testes. These mice probably did not migrate to and from the trapping area, because adjacent lands seemed to afford less favorable habitat for them. During the short season when they were trapped, the mice apparently remained in one small area. The greatest distances recorded between points of capture for various individuals were 10, 20, 28, 38, 60, and 120 yards, respectively. The fall population averaged 3.5 per acre.

Microtus longicaudus

Seven meadow mice of this species were taken from November 10 to January 5, and one was recaptured on April 11. Grinnell & Storer (1924: 125) suggested that *M. montanus* might be active all winter under the snow in the Yosemite region, and this was apparently true of *longicaudus* in our trapping area. They were trapped essentially during the period when green vegetation was absent. Young individuals were taken in November, suggesting late breeding. Some of the mice were taken in the driest parts of the area on piles of bark and rotten logs, others on bare ground, and still others in the most heavily forested parts; the few records indicated no narrow restriction by habitat. The meadow mouse population evidently was low, but more individuals may have been present than were indicated by the trapping records.

Reithrodontomys megalotis

Three harvest mice, two subadult females and one male, were taken July 9 to 15, 1938, and on June 21 and July 21, 1939, respectively. All were caught in the grassiest, most open parts of the trap grids. The species probably is resident in small numbers throughout the year, but certainly is rare in this part of the Sierra Nevada; it first was recorded from Yosemite only recently (Goldman, 1937: 19).

Neotoma cinerea

One subadult female wood rat was caught on August 24, 1938, in the densest stand of timber in the upper grid and, though recaptured in the same trap that afternoon, was not seen thereafter. This record is somewhat below the usual range of the species (Grinnell, 1933: 182) and may represent a wanderer from higher life zones.

Eutamias quadrivittatus

One adult female was caught on October 14, 1938, but was not seen again. She may have been driven down from higher elevation by the approach of unfavorable weather or may have been exploring new territory. It is possible that chipmunks of this species migrate to lower levels in winter. Holdenried (1940: 410) reported eleven individuals of *quadrivittatus* in October 1939 on the same area in which our study was made.

Sciurus griseus

Gray squirrels were seen or heard now and then in the area; none was taken as the traps were probably too small. At least one pair was in residence in 1938 and one or two young were raised somewhere nearby. The squirrels usually remained near large trees, but were sometimes on the ground, feeding on acorns of the black oak. None was observed on the area in winter, and there may be a migration to lower altitudes for the colder season.

Sciurus douglasii

Chickarees were seen several times during August, and six were trapped from September 30 to January 5. Some white fir cones cut by chickarees were used as bait and served to catch at least one individual. On March 30, chickaree tracks were present on the snow, but the animals then were seen infrequently and were unusually silent. There seemed to be about four resident individuals on the area, or about one per acre.

Chickarees were more susceptible to chloroform than any other of the rodents handled, and several died under smaller amounts of anesthetic than used for chipmunks. When trapped, they often injured themselves by battering against the trap doors; this resulted in bloody noses and even fractured skulls. Special trapping and handling techniques evidently would be needed for this species.

Aplodontia rufa

The mountain beaver of the Sierra Nevada normally occurs at higher elevations than our trapping area, but individuals may occasionally follow down the mountain streams in search of new homes or feeding grounds. A young female, about one-fourth grown, was trapped on August 17, on a dry and rather open hillside between two large logs and at least 100 yards from water. After marking, it was

released and started off almost directly downhill towards the creek, occasionaly stopping to eat the herbage of bracken, thimbleberry, gooseberry, and monkeyflower. Arriving at the edge of the water, it plunged in without hesitation and swam upstream near the bank. Then, emerging, it walked along the bank and disappeared into a hole in the rocks. There has been some controversy in the past as to whether Aplodontia really swims or takes to water readily. Vernon Bailey (1936: 226) has recorded two other instances of swimming by these rodents.

THE RODENT POPULATION AND ITS FOOD REQUIREMENTS

From our data on the various rodent species active in the Bass Lake study area, the fluctuations in total numbers of active individuals per acre have been calculated (Fig. 6). The size of this population during four representative periods of the year was determined to be as follows: April 1-30, 26.8 individuals per acre; July 18-Aug. 8, 60.0; Sept. 15-Oct. 15, 33.1; and Dec. 1-31, 20.9. The population in mid-summer thus included nearly three times as many individuals as in winter. Numbers alone are of interest, but may be misleading if the gross effect of a population is to be considered quantitatively. It is desirable, therefore, to express the population also in terms of its weight or bio-mass and of its food requirements. This obviously is important in considering the effect of rodents on vegetation and the total amount of "rodent" available as food for predatory animals.

Lacking sufficient data on the weights of the local rodents, we have assumed crude averages from weights given in Grinnell and Storer (1924) for the same species in the Yosemite region slightly north of Bass Lake. For simplicity the average weights of individuals are assumed to be the same throughout the year, but we realize that the young when first abroad weigh less than adults and that all individuals gain in weight as the warm season proceeds, especially with the accumulation of fat. The average weights per acre, by species, for the above-mentioned periods are shown in Table 1; the totals of all species were as follows: April 1-30, 5.1 kilograms; July 18-Aug. 8, 10.7 kg.; Sept. 15-Oct. 15, 5.6 kg.; Dec. 1-31, 1.5 kg. The number of individuals active in winter is reduced to one-third of the summer peak, whereas the total rodent weight is down to one-sixth of the summer maximum. In terms of pressure on rodent food and also of the food supply for predators, this is a much more drastic decrease than numbers alone would suggest; it results from the fact that the larger rodent species at Bass Lake hibernate and only the smaller ones are active in the winter. It may explain also why some carnivorous birds and mammals are less numerous in the yellow pine belt during the winter. They must migrate or hibernate (bears) to compensate for local food shortage.

With these rather imperfect data on the bio-mass of rodents we may estimate the food requirements of the rodent population. Unfortunately there are few data of any sort on the amounts of food consumed by rodents in nature. The several species on the Bass Lake area differ considerably in their food habits, from the subterranean gophers that eat roots and some stems, through the ground squirrels and mice with more varied diets including many seeds and fruits, to the tree squirrels that subsist extensively on conifer seeds. Lacking field data, the problem has been approached indirectly. Kleiber (1933) states that the food requirement of a mammal is proportional to the ¾ power of its body weight *i.e.*, to its metabolic body size. The amount of food consumed per day, divided by the metabolic body size, gives the relative food intake. On this premise, if the relative food intake has been determined for one species as a standard, the amount theoretically consumed by any other species of known weight on an essentially similar diet will be the product of its metabolic body size and the standard relative food intake.

None of the rodent species in the Bass Lake study area could serve as a standard because there were no data on food intake. We have, therefore, had recourse to two different sets of observations which might serve as fair bases for estimating the food requirements of this wild population. Kleiber and

TABLE 1. Active rodent population in numbers and weights per acre, Bass Lake area, 1938-1939.

Species	Assumed Average wt. (kg.)	Numbers per acre				Weights per acre (kg.)			
		April 1-30	July 18 Aug. 8	Sept. 15 Oct. 15	Dec. 1-31	April 1-30	July 18 Aug. 8	Sept. 15 Oct. 15	Dec. 1-31
Peromyscus maniculatus	.025	8.0	16.8	9.6	8.5	.200	.420	.240	.213
Peromyscus boylii	.025	3.0	15.2	2.8	1.6	.075	.380	.070	.040
Eutamias quadrimaculatus	.090	1.8	1.2	1.0	—	.162	.108	.090	—
Citellus beecheyi	.500	7.4	17.2	7.2	—	3.700	8.600	3.600	—
Thomomys bottae	.080	4.8	8.2	9.0	8.8	.384	.656	.720	.704
Perognathus californicus	.025	—	—	1.4	—	—	—	.035	—
Microtus longicaudus	.040	0.4	—	—	0.8	.016	—	—	.032
Sciurus griseus	.800	0.4	0.4	0.6	0.4	.320	.320	.480	.320
Sciurus douglasii	.250	1.0	1.0	1.5	0.8	.250	.250	.375	.200
Total numbers	...	26.8	60.0	33.1	20.9	...	...	...	...
Total weights	...	....	....	....	....	5.1	10.7	5.6	1.5

Smith (1940) found that individuals of a laboratory strain of *Rattus norvegicus* when about 161 grams in average weight (91 days old) ate 14 to 15 grams of a stock ration that was relatively concentrated and scant in roughage. Ranson (1934) stated that the daily ration of captive *Microtus agrestis* weighing about 30 grams consisted of 10 grams of herbage, 6 grams of roots and 3 grams of cereals for a total of about 19 grams. Reduced to an air-dry basis these two diets average 13.0 and 5.7 grams, respectively.[1]

The *Microtus* diet may approximate more nearly the natural "average rodent diet"; but both diets probably are below average in quantity because animals in captivity are thought to expend less energy than those free in nature. The metabolic body size in kilograms to the ¾ power was 0.07 for *Microtus agrestis* and 0.25 for *Rattus norvegicus*. The relative food intake was calculated as the dry weight of food consumed divided by the metabolic body size, thus: *Microtus*, $5.7 \div 0.07 = 81$ grams/kilogram (henceforth called the "A" standard); *Rattus*, $13.0 \div 0.25 = 52$ grams/kilogram ("B" standard). The discrepancy between the standards probably arises from differences in digestibility of the two diets. Both are used in the calculations (Table 2) for estimates of daily food consumption by the Bass Lake species.

The total daily food consumption (dry weight) per acre, on the "A" standard would vary from 0.21 kg. in December to 1.17 kg. in July; and on the "B" standard, from 0.15 kg. in December to 0.74 kg. in July.[2]

These two sets of figures indicate the order of magnitude of the total daily consumption of food on a dry weight basis.

Since rodent use of forage is viewed competitively by owners of range livestock, a crude comparison of the two categories of animals may be attempted. The 23.5 pounds (10.7 kg.) of rodents, per acre, in summer, eat 1.6 to 2.6 pounds (0.74 to 1.17 kg.) daily on a dry food basis, and a 750 pound (342 kg.) steer needs about 14 pounds (6.4 kg.) per day. Thus the rodents on one acre collectively require from 12 to 18 per cent as much as a beef animal, or those on 5½ to 8½ acres have a food demand equivalent to that of one average steer.

By making more assumptions it would be possible to carry such comparisons farther; perhaps too many have already been made. Nevertheless, so far as we know, an estimate, in terms of food consumption, of the pressure exerted by the *total population* of rodents on an area is not available elsewhere. Yet this is the ultimate goal towards which most rodent studies of range ecology are directed. We hope that

[1] Calculated as follows:

	Total weight (grams)	Water content (per cent)	Dry weight (grams)
(A) *Microtus diet*			
Herbage	10	75	2.5
Roots	6	88	.7
Cereals	3	15	2.5
(B) *Rattus diet*			
Concentrated	14.5	10	13.

[2] Assuming the dry matter to represent 30 per cent of the "average rodent diet" (from the *Microtus* or "A" standard), the gross daily food consumption, per acre would approximate 0.7 (A) or 0.45 (B) kg. in December, and 3.8 (A) or 2.5 (B) kg. in July or about 1 to 1½ pounds of "fresh" food in winter and 5½ to 8 pounds in midsummer.

TABLE 2. Calculated daily food intake (dry basis) per acre of Bass Lake Rodents.

Species	Assumed average weight (kg.)	Metabolic body size (kg.¾)	Individual food intake (kg.) Standard A[1]	Individual food intake (kg.) Standard B[2]	A Standard April 1-30	A Standard July 18 Aug. 8	A Standard Sept. 15 Oct. 15	A Standard Dec. 1-31	B Standard April 1-30	B Standard July 18 Aug. 8	B Standard Sept. 15 Oct. 15	B Standard Dec. 1-31
Peromyscus maniculatus	.025	0.06	.005[3]	.003[4]	.040	.084	.048	.042	.024	.050	.029	.025
Peromyscus boylii	.025	0.06	.005	.003	.015	.076	.014	.008	.009	.045	.008	.005
Eutamias quadrimaculatus	.090	0.16	.013	.008	.023	.016	.013	–	.014	.010	.008	–
Citellus beecheyi	.500	0.60	.049	.031	.363	.843	.353	–	.229	.533	.223	–
Thomomys bottae	.080	0.15	.012	.008	.058	.098	.108	.106	.038	.066	.072	.070
Perognathus californicus	.025	0.06	.005	.003	–	–	.007	–	–	–	.004	–
Microtus longicaudus	.040	0.09	.007	.005	.003	–	–	.006	.002	–	–	.004
Sciurus griseus	.800	0.85	.069	.044	.028	.028	.041	.028	.018	.018	.026	.018
Sciurus douglasii	.250	0.35	.028	.018	.028	.028	.042	.022	.018	.018	.027	.014
TOTALS	....	....	0.19	0.12	0.56	1.17	0.63	0.21	0.35	0.74	0.40	0.14

Total daily food consumption per acre (kg.) (Numbers of rodents from Table 1)

[1] A standard (Microtus, wt. 30 g., food 5.7 g., relative food intake .081 kg.)
[2] B standard (Rattus, wt. 161 g., food 13.0 g., relative food intake .052 kg.)
[3] .081 x 0.06 = .005, etc.
[4] .052 x 0.06 = .003, etc.

this tentative expression of food requirements will at least serve to emphasize the need for more accurate information.

SUMMARY

LAKE TAHOE

1. Studies on the natural history of rodents were carried on from May 19 to October 31, 1937, about Lake Tahoe, California.

2. Methods of study included visual counts of diurnal rodents, permanent and moving lines of snap traps, and live traps to capture individuals which were marked and released. Each live rodent was anesthetized in a glass jar, by use of an atomizer to facilitate handling the animal and permit removal of ectoparasites at each capture.

3. An experiment at elimination by snap traps near Myers demonstrated the ability of rodents to "fill up" territory which had previously been rendered vacant. In June, 91 rodents were removed; a second trapping in August produced 83 invaders, indicating a 92 per cent "recovery"; and a third trapping in September-October yielded 21 additional rodents.

4. Snap traps were used near Carnelian Bay to test the efficiency of routine poisoning for rodent control as practiced by official agencies. In July, shortly after distribution of poison, only 3 tree squirrels were taken. In September the same area yielded a total of 17 rodents, 43 then were taken on a similar, unpoisoned control area. Re-invasion of vacant territory again was indicated.

5. Live trapping on another area near Myers in August yielded 40 rodents before poisoning and 5 afterward. Live traps near Al Tahoe caught 102 rodents in June, just before poisoning, and only 27 in August.

6. Watch was kept throughout the season for dead mammals and birds in poisoned areas. Only two dead birds were found, and no mammals other than rodents.

BASS LAKE

1. The total rodent population of 2.3 acres near Bass Lake, Madera County, California, was studied from July 6, 1938 until July 8, 1939.

2. Several types of live traps were used; the animals were anesthetized, marked, and released according to the methods previously developed at Lake Tahoe. Trapping was done in grids, with a total of 23,653 trap nights and 26,771 trap days. The baits were mainly rolled oats, but pine nuts, sunflower seeds, raisins, and peanuts were used occasionally.

3. Of 13 species present, 4 comprised 60 per cent of the population from April to early October. The gross population per acre varied from 19 in late December and March to 60 in late July and early August. At the July peak, the bulk of the population consisted of *Peromyscus maniculatus, P. boylii, Citellus beecheyi,* and *Eutamias quadrimaculatus;* decline in the autumn was due to the disappearance of the latter three species.

4. In December and March approximately 90 per cent of the population consisted of residents, but in mid-summer the transients and non-residents comprised almost 40 per cent of the population. The percentage of immatures in the population showed a similar trend.

5. The study area was buried under deep snow from January 5 to late March, when there was no green vegetation except on the conifers. Grasses began to appear by March 31 and were abundant by early May. Prominent sources of food through the summer were lupines, gooseberries, dogwood, and elderberries. The rodent food supply was particularly plentiful in mid-summer and at no time seemed insufficient to support the active individuals present.

6. The chief food competitors of the rodents were cattle, a few deer, and several species of fruit- and seed-eating birds.

7. There was scant evidence of predation; the predatory species present included weasels, pine marten, gray fox, skunk, black bear; red-tailed, Cooper and sharp-shinned hawks; horned and screech owls; rattlesnakes, rubber and garter snakes, and racers.

8. *Peromyscus maniculatus* was active throughout the year and was apparently the commonest local rodent. It had two peaks of reproductive activity, in mid-summer and autumn. Young *maniculatus* underwent a post-juvenal molt which required 8 to 35 days. Adult individuals had home ranges of about one-quarter acre. The numerous and varied movement by individuals were classified as follows: short journeys from established home range, slow but constant shift of home range, immigration, transient movements, search for new homes by young, and extension of range for feeding. The resident population per acre varied from 5 in June to 10 in July and August.

9. *Peromyscus boylii* had a more definite season of activity; from late autumn to early spring it was captured only in small numbers. There was but a single peak of breeding, in June. In movements and establishment of home range, this species was similar to *maniculatus,* but its population included a larger non-resident element than *maniculatus.* In the first half of September the non-residents made up 70 per cent of the population. The total resident population per acre varied from 0.8 in November to 7 in June.

10. *Eutamias quadrimaculatus* had a marked season of activity and hibernated during the cold weather. Home ranges averaged at least one acre for adult females and two acres for adult males. There was little evidence of non-resident individuals. The active population per acre varied from 0.5 in April to 2.5 in June.

11. *Citellus beecheyi* proved similar in many habits to Eutamias but had a home range only about one-half as large. The total population per acre ranged from about 7 in April to 17 in July.

12. *Thomomys bottae* was represented by 17 individuals taken in traps on the ground surface; the

captures were too few to ascertain the local population of the species.

13. Species represented less commonly or by single captures were: *Perognathus californicus, Microtus longicaudus, Reithrodontomys megalotis, Neotoma cinerea, Eutamias quadrivittatus, Sciurus griseus, Sciurus douglasii,* and *Aplodontia rufa.*

Rodent Population and its Food Requirements

1. The total number of rodents per acre at Bass Lake varied from 60 in July-August to 20.9 in December; the average total weight per acre was estimated at 10.7 and 1.5 kg., respectively, for these two periods. The winter decrease was therefore twice as great, in terms of its bio-mass, as in numbers of individuals.

2. Assuming that the food requirement of an animal is proportional to the ¾ power of its body weight, the total daily food consumption (dry weight) per acre of the Bass Lake rodents was estimated at 0.74 to 1.17 kg. in July and 0.14 to 0.21 kg. in December. The July figures represent from 12 to 18 per cent as much food as is required by a 342 kg. steer.

LITERATURE CITED

Bailey, V. 1936. The mammals and life zones of Oregon. U.S.D.A., Bur. Biol. Surv., N. Amer. Fauna **55:** 1-416, 102 figs., 52 pls., 1 map.

Clark, F. H. 1938. Age of sexual maturity in mice of the genus Peromyscus. Jour. Mamm. **19:** 230-234.

Collins, H. H. 1918. Studies of normal moult and of artificially induced regeneration of pelage in Peromyscus. Jour. Exp. Zool. **27:** 73-99, 2 pls., 15 figs.

Edge, E. R. 1931. Seasonal activity and growth in the Douglas ground squirrel. Jour. Mamm. **12:** 194-199, 2 pls., 1 fig.

Goldman, R. 1937. A new rodent record in Yosemite. Yosemite Nature Notes **16** (March): 19.

Gordon, K. 1936. Territorial behavior and social dominance among the Sciuridae. Jour. Mamm. **17:** 171-172.

Gordon, K. 1938. Observations on the behavior of Callospermophilus and Eutamias. Jour. Mamm. **19:** 78-84, 2 figs.

Grinnell, J. 1933. Review of the recent mammal fauna of California. Univ. Calif. Publ. Zool. **40:** 71-234.

Grinnell, J. & T. I. Storer. 1924. Animal life in the Yosemite. Berkeley, xviii + 752 pp., 65 figs., 60 pls., 2 maps.

Holdenried, R. 1940. A population study of the long-eared chipmunk (Eutamias quadrimaculatus) in the central Sierra Nevada. Jour. Mamm. **21:** 405-411.

Johnson, B. W. 1927. Preliminary experimental studies of mice of Mount Desert Island, Maine. Jour. Mamm. **8:** 276-284.

Kleiber, M. 1933. Tiergrösse und Futterverwerbung. Die Tierernährung **5:** 1-12.

Kleiber, M. & A. H. Smith. 1940. Eating habits and fasting metabolism of rats. Proc. Soc. Exp. Biol. and Med. **45:** 630-634.

McCoy, G. W. 1912. Notes on the bionomics of rats and ground squirrels. U. S. Publ. Health Repts. **27:** 1070.

Meyer, K. F. 1938. Sylvatic plague. Amer. Jour. Publ. Health **28:** 1153-1164.

Osgood, W. H. 1909. Revision of the mice of the American genus Peromyscus. U.S.D.A., Bur. Biol. Surv., N. Amer. Fauna **28:** 1-285, 12 figs., 8 pls., 1 map.

Ranson, R. M. 1934. The field vole (Microtus) as a laboratory animal. Jour. Anim. Ecol. **3:** 70-76.

Ross, R. C. 1930. California Sciuridae in captivity. Jour. Mamm. **11:** 76-78.

Schooley, J. P. 1934. A summer breeding season in the eastern chipmunk, Tamias striatus. Jour. Mamm. **15:** 194-196.

Storer, T. I. & P. W. Gregory. 1934. Color aberrations in the pocket gopher and their probable genetic explanation. Jour. Mamm. **15:** 300-312.

Sumner, F. B. 1917. Several color "mutations" in mice of the genus Peromyscus. Genetics **2:** 291-300.

Svihla, A. H. 1932. A comparative life history study of the mice of the genus Peromyscus. Univ. Mich. Mus. Zool. Misc. Publ. **24:** 1-39.

Svihla, A. H. 1935. Development and growth of the prairie deer-mouse, Peromyscus maniculatus bairdii. Jour. Mamm. **16:** 109-115.

A COMMUNITY STUDY OF A DISTURBED DECIDUOUS FOREST AREA NEAR CLEVELAND, OHIO, WITH SPECIAL REFERENCE TO INVERTEBRATES

W. W. Dowdy
Lincoln University, Mo.

Submitted in partial fulfillment of the requirements for the Degree of Doctor of Philosophy by Western Reserve University, June, 1942.

TABLE OF CONTENTS

A COMMUNITY STUDY OF A DISTURBED DECIDUOUS FOREST AREA NEAR CLEVELAND, OHIO, WITH SPECIAL REFERENCE TO INVERTEBRATES

INTRODUCTION

The approach to this study is biotic. The invertebrates, however, have received special emphasis. The study was started October 19, 1939 and continued to September 10, 1940. A collecting station was established at each place in the area which presented a different kind of plant community. Each station was selected after examination of the area and located in representative areas of the communities to be studied. The location of each station is indicated on the accompanying map of the area studied. Five stations were established, each in a different community. The communities are listed in successional order:

Potentilla-Solidago-Rumex Associes (Station I)
Solidago-Agrostis-Daucus Associes (Station II)
Quercus-Carya Associes (Station III)
Acer-Tilia-Sambucus Associes (Station IV)
Fagus-Acer Association (Station V)

Invertebrates were collected at each station at approximately weekly intervals. In these collections one soil sample was taken each time, it consisted of material from 0.1 of a square meter to a depth of three inches, the area was measured with an iron ring. Samples of herbs and low shrubs were made with an insect net (48 sweeps = 1 square meter). The diameter of the net was 20 inches, the depth 26 inches. These two types of collections were made from each station at about the same time of the day and week. The soil samples and sweeps were taken into the laboratory and washed and sorted for the invertebrates that might be present. The washing was done through a series of sieves or screens, one placed on top of the other, the screen with the largest mesh at the top, the next size mesh immediately beneath, etc. The specimens were placed in vials with apropriate labels. During most of the winter months there were no herb or low shrub samples.

The relative humidity and temperatures were taken at each station, weekly, at the same time the invertebrates were collected. Rain gauges and maximum-minimum thermometers were placed at Stations I and V, and their readings recorded each week. The rain gauges were similar to the United States Weather Bureau type, but smaller and perhaps not as accurate. The maximum-minimum thermometers were the registering six pattern, differential, wall form. In taking the relative humidity the cog psychrometer and government tables were used.

The area studied is located about 14 miles east of the city limits of Cleveland. It is bordered on the north by Mayfield Road, on the south by Cedar Road, on the east by S. O. M. Center Road and on the west by Lander Road (Longitude 81° 30′ Latitude 41° 30′). The entire area is about 1.3 miles square and within its boundary are a number of houses, streets and roads, as the accompanying map will show. These have done much to disturb the balance within the community and its species composition. The area under study has also been disturbed by hunters, woodcutters, picknickers, berry-pickers, fires, realtors and cemeteries, the latter still in use. One of the old residents of the community informed the author that about twenty years ago most of the fields were under cultivation. The fields still show signs of earlier cultivation through the old furrows that are now covered with vegetation. At present only a few small gardens and two or three corn patches of from one to two acres are cultivated.

Hesse *et al.* (1937) maintain that primitive man interfered with conditions of his environment relatively little, yet his activities affected animal distribution. According to these writers civilized man changes his environment greatly; he destroys many kinds of habitats and replaces them with others.

Shelford (1937) states that civilized man's operations interfere with animals and animal habitats; his first work is to destroy all large, dangerous animals. Man clears and cultivates the land, bringing death and destruction to many more. Shelford maintains that animal communities are divisible into primeval or primary communities, and man-made, or secondary communities.

Wellhouse (1936) holds that our increasing losses through insects are due to advance of civilization. He maintains that as we bring more and more wild land into cultivation we reduce the number and kinds of plants growing on it. Insects which formerly had dozens of wild plants to browse upon now congregate on the few tender ones which have been substituted and often damage or destroy them.

Van Deventer (1939) concludes that man-created and controlled conditions are suitable not only for man and his domestic animals, but also for a series of wild animal species including representatives of all land-dwelling groups; invertebrates, amphibians, reptiles, birds, and mammals.

Clements & Shelford (1939) maintain that man, as a superdominant may exert all the reactions caused by animals and nearly all those due to plants, working more or less directly through his own activities. When his innumerable coactions enter the scene, he becomes also a superinfluent, with the reactions of plants and animals as well as of the entire community at his command.

The historical development of the concept biotic

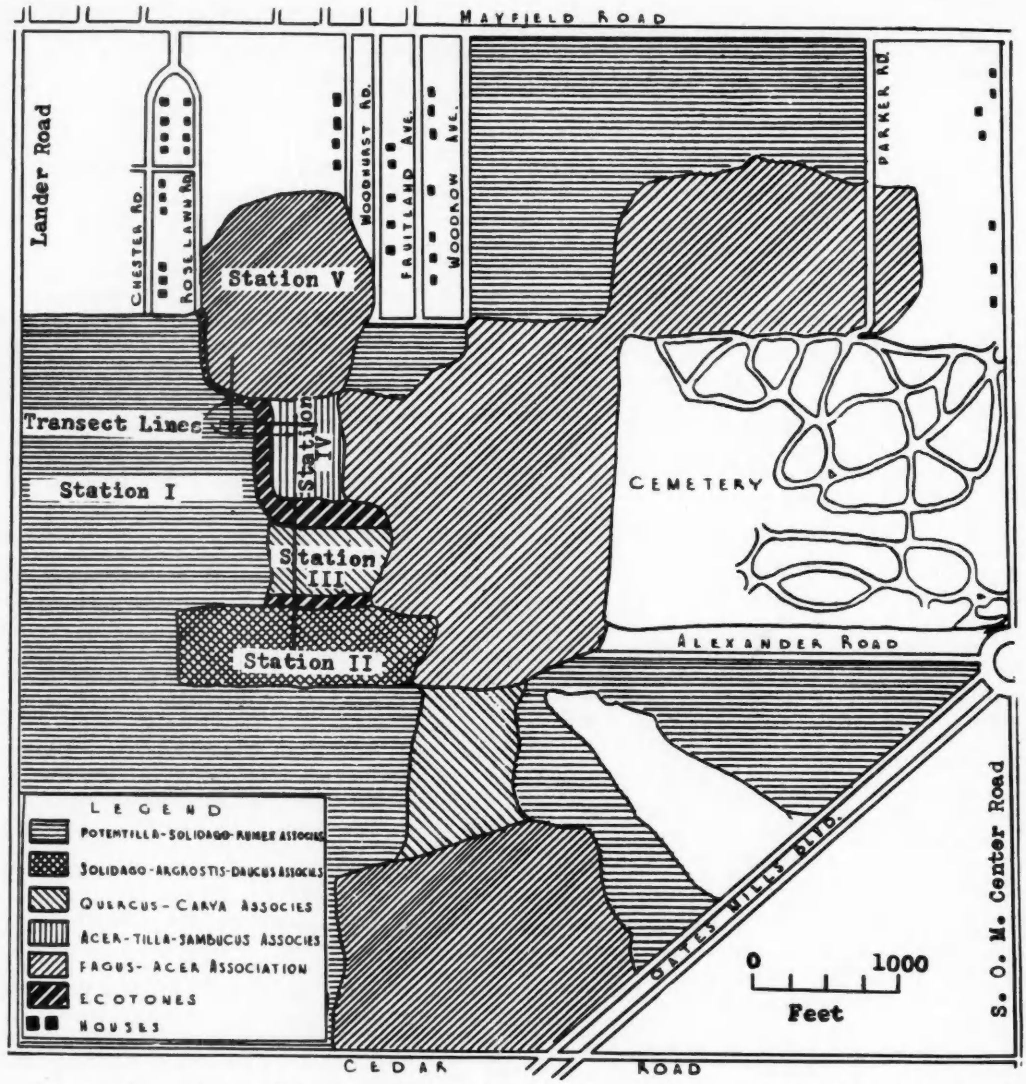

Fig. 1. Map of area studied, showing location of stations and similar areas, based on aerial photograph.

community has been outlined, in some detail, by Clements & Shelford (1939).

Weaver & Clements (1929) discuss the deciduous forest formation and maintain that the beech-maple forest is the typical association of this formation.

The author wishes to express his grateful appreciation to Dr. H. B. Roney who suggested the problem and under whose direction the work was done. The author also wishes to acknowledge his indebtedness and to express thanks to the following specialists in the taxonomic determination of material belonging to special groups: Paul Bartsch, Mollusca; J. O. Maloney, Isopoda; R. A. Hefner and R. V. Chamberlin, Myriapoda; R. V. Chamberlin and W. M. Barrows, Araneida; H. E. Ewing, Thysanura; Grace Glance, Collembola; A. B. Gurney, Orthoptera and Neuroptera; H. G. Barber and H. H. Knight, Hemiptera; P. W. Oman and P. W. Mason, Homoptera; W. H. Anderson, J. N. Knull, C. A. Frost, R. E. Blackwelder and P. C. Ting, Coleoptera; Carl Heinrich, J. F. Gates Clarke and H. W. Capps, Lepidoptera; C. T. Greene, Alan Stone and D. G. Hall, Diptera; C. F. W. Muesebeck, R. A. Cushman, K. V. Krombein and L. H. Weld, Hymenoptera and Mrs. I. T. Frary, the grasses of the area.

ENVIRONMENTAL ANALYSIS

GEOLOGY AND SOIL

The rock belongs to the Cuyahoga group; this group consists of Meadville shale, Orangeville shale and Sharpville sandstone. However, within the area the rock is mostly Orangeville shale with a top-covering of ground moraine. The predominating soil is the Mahoning silty clay loam. This is a glacial soil drift from shale and sandstone material.

Samples of the first 3 inch layer of the soil were taken and thoroughly mixed and analyzed. The soil was tested by the Hellige-Troug method and the apparatus was the Hellige-Troug combination soil tester. The pH at all stations was 5, except Station IV which had a pH of 4.5; the latter station seemed to be somewhat lower and held water longer than the other stations. The soil at Station I was low in phosphorus, at all other stations it was very low in phosphorus. Potassium was medium to high at all stations. Nitrate at Stations II and III was almost none, at Stations IV and V very low and at Station I there was none. Calcium was low at all stations. Ammonia at Stations I and IV was very low, at Stations II and III low, and at Station V low to medium.

DRAINAGE

The Mahoning soils have very heavy relatively impervious subsoils which make underdrainage difficult. The eastern half of the area drains in a northeastern direction and finally empties into the Chagrin River. The western half drains toward the west and empties into Euclid Creek. In general, the drainage is poor, hence for several days after the rains much water still remains in hollows and pockets; these depressions are more numerous in the woods than in the fields; some are made by uprooted trees. The woods are usually damp and very seldom approach a dry condition. In the spring numerous typical temporary ponds develop throughout the area.

The highest altitude above sea level (1,140 feet) is located at the corner of S. O. M. Center and Cedar Roads, the southeastern corner of the area. The lowest point above sea level (1,050 feet) is located at the corner of Mayfield and S. O. M. Center Roads, the northwestern corner of the area. Otherwise the area is fairly level, although in some parts it is slightly rolling.

CLIMATE

TEMPERATURES

Williams (1936) maintains that the close proximity of Lake Erie may be a factor modifying, to some extent, the climate of the region and that the temperatures do not rise so high nor fall so low near the lake as farther inland. He also cites Mosely (1897) as maintaining that the lake is often responsible for a condition of cloudiness that diminishes very appreciably the amount of available sunshine.

In this study there was a decrease in the mean monthly temperature from October 19, 1939 (the beginning of this work) through January. The lowest mean monthly air temperature (all stations combined) was 21.11° in January. From February through July the mean monthly air temperature increased each month until it reached 76.6° in July. Beginning in August there was a gradual falling off in the mean monthly temperature.

Temperatures were taken about 4.5 feet above the ground, called air temperatures; on the surface of the ground, called surface temperatures; by inserting the point of the thermometer about one inch beneath the surface, called soil or ground temperatures. From these temperature records the following facts were revealed:

(1) Air temperature, during the winter, goes much lower than temperatures on the surface or in the ground, frequently much below freezing.

(2) Surface temperatures rarely go below freezing; when they do the difference is very slight, not exceeding one or two degrees below. This, at least, was the case in this work which might be due to the fact that the ground was covered with a deep blanket of snow, most of the winter, and sometimes with a layer of ice and vegetation beneath the snow.

(3) Ground temperatures, as a rule, did not go much below freezing, but quite frequently approached the freezing point.

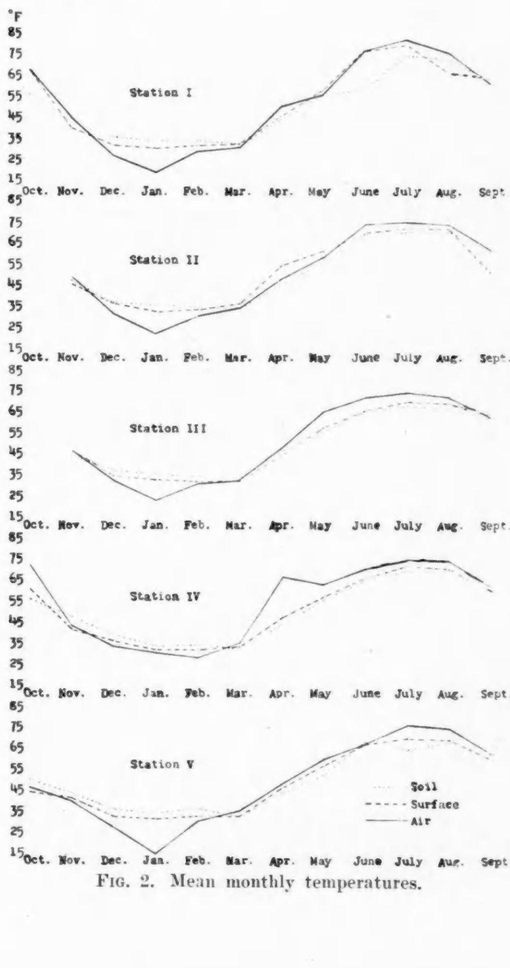

FIG. 2. Mean monthly temperatures.

(4) The graphs on the temperature records will show that the ground is much warmer in the winter and much cooler in the summer than the surface or air above.

(5) This condition of the earth, being warmer in the winter and cooler in the summer than the outside, affords a great protection to invertebrate life, especially to numerous insects which are found in the ground during the winter; the ground is just as important a factor during the summer, as during the winter, as a place of protection for many invertebrates against high air temperatures. Hess (1937) maintained that temperatures above 60° usually prove fatal to *Lumbricus terrestris* L., and Walton (1928) said that temperatures of 75° or higher are quickly fatal to earthworms under most conditions.

(6) The surface of the ground in the winter also affords protection to the life of such invertebrates that are not able to penetrate below the surface. Such invertebrates crawl under objects and vegetation on the ground where they find the temperature much higher than the temperature of the air above. Such invertebrates (those taking cover under objects, etc., at the surface) may also be afforded great protection during the summer months against unusually high air temperatures.

MAXIMUM AND MINIMUM TEMPERATURES

Based on records from Station I the lowest maximum temperature recorded was 29° on January 4, and the lowest minimum temperature at the same station was —12° on January 27. The highest maximum temperature at Station I was 114° on August 21, and the highest minimum temperature 62.2° on June 12. At Station V, the beech-maple association, the lowest maximum temperature was 29° on January 3, and the lowest minimum temperature at the same station was —1.5° on February 1. The highest maximum temperature at Station V was 105° on May 16, and the highest minimum temperature at the same station was 72° on August 15. The figures in tabular form follow:

	Station I Field	*Station V Woods*
Lowest maximum	29° F.	29° F.
Lowest minimum	—12° F.	—1.5° F.
Highest maximum	114° F.	105° F.
Highest minimum	62.2° F.	72° F.

These figures indicate that lower temperatures were reached during the winter and higher temperatures were reached during the summer in the open field than in the woods. This is clearly shown when the lowest minimum and the highest maximum are compared in the field and woods in the above tabular data.

During extreme temperatures the biotic community is afforded better protection in the woods than in the field.

PRECIPITATION

On October 18, the first light frost appeared which was followed by a killing frost on November 11. On October 24, the first sleet fell which was followed by snow on October 28. For November and December the snowfall was below normal. January, February, March and April were markedly above normal in the amount of snowfall but May had no snow at all; trace is normal for May. The total amount of snowfall for the winter of 1939-1940 was 55.0 inches, whereas 40.1 inches would be normal for Cleveland.

According to Williams, the Cleveland Station of the United States Weather Bureau gives 200 days as the length of the growing season in this locality.

The total amount of rainfall at Station I, Potentilla-Solidago-Rumex Associes, from October 19, 1939 to September 10, 1940, was 29.35 inches.

The total amount at Station V, the beech-maple association, for the same period of time was 31.83 inches.

The total amount of rainfall reported by the Cleveland Weather Bureau from October 1, 1939 to September 30, 1940 was 29.37 inches. Normal for Cleveland is 34.55 inches.

RELATIVE HUMIDITY

The mean monthly relative humidity ranged from 59.0 to 93.0 per cent, with the winter months somewhat higher than the summer months. Readings were made as high as 100 per cent at Stations V and IV on March 6 and May 3; 100 per cent readings were also made at Station II on March 4, and at Station III on April 12. No 100 per cent readings were ever taken at Station I, the field. Some very low readings were recorded on April 24: Station V, 43 per cent; Station IV, 38 per cent; Station III, 34 per cent; Station II, 38 per cent; and Station I,

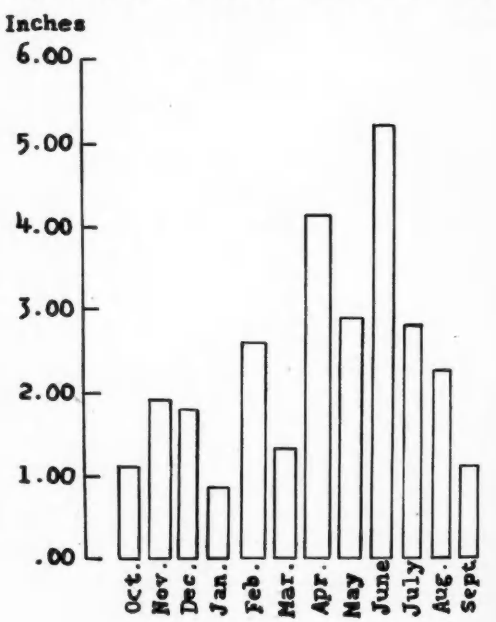

Fig. 3. Rainfall at Station I.

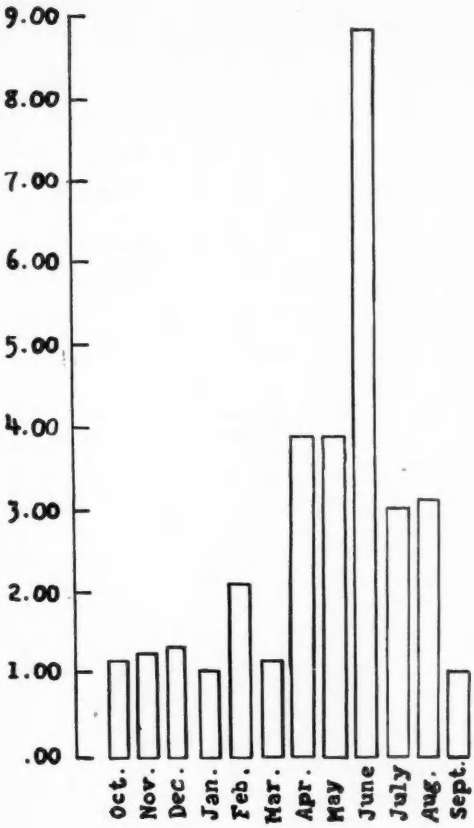

FIG. 4. Rainfall at Station V.

61 per cent. The lowest at Station I, the field, was 51 per cent on May 22.

The data indicate that at Station I, the field, the relative humidity never fluctuated as much as in the woods.

A comparison of the mean relative humidity at the stations, for the entire period of study, shows the following data: Station I, 73.7 per cent; Station II, 73.6 per cent; Station III, 76.2 per cent; Station IV, 73.6 per cent; Station V, 76.2 per cent; all stations combined, 74.6 per cent; Weather Bureau 73.4 per cent.

WIND

According to the Weather Bureau from April 1939 through September 1940, the prevailing direction of the wind, by month was as follows: southwest, five months; south, four months; northwest, two months; southeast, four months; northeast, one month; west, one month; north, one month. The average hourly velocity in miles over the same period of time, varied from 11.2 to 17.4 miles per hour. The total movement varied between 7,000 and 13,000 miles per month. Both the velocity and the total movement

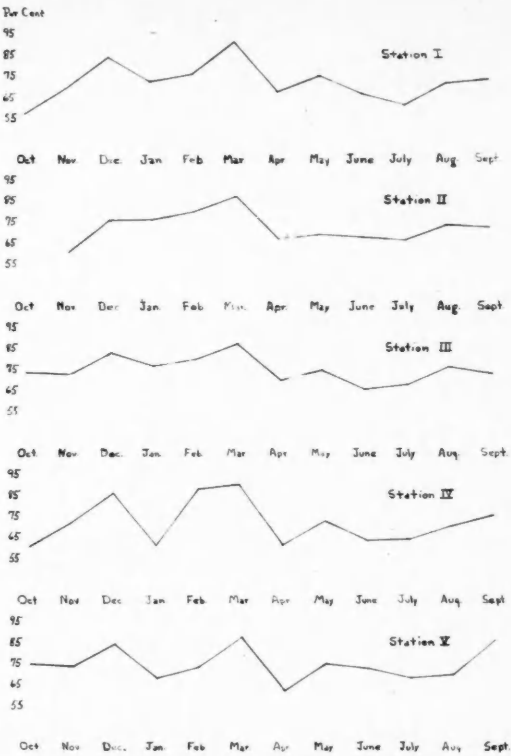

FIG. 5. Showing relative humidity, mean monthly, at each Station.

showed a very marked decline from December to September.

SUNSHINE

According to the Weather Bureau, the amount of sunshine, by month, from April 1939 through September 1940, varied between 19 and 79 per cent. The amount of sunshine decreased from October through January but there was a gradual increase from February through July, after the latter month there was again a gradual decrease in the amount of sunshine. On the whole the colder months appear to have less sunshine. From December through March the percentage of sunshine was less than normal for Cleveland; May was also less than normal.

COMMUNITY ANALYSIS

COMMUNITIES OF THE AREA

In the vegetation study line transects and chart quadrats were used.

Three transects were made (Fig. 1): The first, 470 meters long, extended north and south through Stations IV, III, and II; the second, 200 meters long, extended east and west through Stations I and IV; the third, 150 meters long, extended north and south through Stations I and V. The vegetation was

counted in units of two meters on each side of the transect line and one meter along the line; each unit being four meters by one meter.

Three quadrats of herb counts, one meter square, were made at each station or each community, making a total of 15 quadrats for the area under study.

On the basis of the foregoing transects and quadrats five communities have been designated.

Each community will now be discussed in successional order.

POTENTILLA-SOLIDAGO-RUMEX ASSOCIES (STATION I)

This station was located in the open field, which had not been under cultivation over a period of approximately fifteen to twenty years. It is now being invaded by seedlings of sumac, aspen, elm, and wild cherry. The field is adjacent on the north to the Fagus-Acer Association in which Station V was located. On the east it is adjacent to the Acer-Tilia-Sambucus Associes in which Station IV was located, and on the southeast to the Quercus-Carya Associes in which Station III was located. Station I was not adjacent to Station II since the Quercus-Carya Associes was located between Stations I and II (Fig. 1). A dirt road, which is still in use, ran along the northern border of the field in which Station I was located. Some of the collections at Station I were made within forty meters of this road. Another dirt road intersected the former and ran completely across the field in a northeastern direction into Station III. Some of the collecting at Station I was done within fifteen meters of this second road.

Within the borders of the station, particularly immediately south of the northern dirt road, the terrain was irregular and held water in the depressions for long periods of time. Care was taken to omit these more mesic areas when studying the community type which was relatively much drier. In such small areas facies or consocies of Carex and mosses occurred, constituting in total a considerable portion of the area.

From thirty-five to forty ant mounds about 1.5 feet high by two feet wide were located about this station. These mounds on the average were about fifteen or twenty meters apart. These ants were *Formica fusca*, var. *subsericea* Say.

Vegetation

The dominants here are Potentilla, *Solidago canadensis* L. and *Rumex* sp. The map (Fig. 1) shows that a good portion of the area, about 30 per cent, is similar in vegetation to that surrounding Station I.

Of the three dominants, the golden rod had a more regular distribution throughout the area than the other two; golden rod is recorded on both transects, and 26.6 per cent on the quadrats. Potentilla and Rumex are recorded only on the quadrat, the former 21 per cent, the later 13.6 per cent. Sporadic distribution was characteristic of these two dominants and also true of the subdominants. This was perhaps the reason why some plants were recorded on the quadrat and not on the transect and vice versa.

The subdominants listed in order of abundance were as follows:

1. *Chrysanthemum leucanthemum* L: This was one of the earliest plants to be in leaf at this station.
2. *Fragaria virginiana* Duchesne: This species remained close to the ground and was never more than four or five inches high. It had a fairly even distribution within the area, as it was recorded on both transects and the quadrat.
3. *Agrostis alba* L: This grass was recorded on the transect and the quadrat, and was more abundant in the low wet places and about old roads than elsewhere.
4. *Danthonia compressa* Aust: This species was also recorded on the transect and the quadrat, and like *Agrostis alba*, was more abundant in the low wet places and about old roads than elsewhere.
5. Prunella: This genus was recorded on the quadrat only and was not very abundant (about 6 per cent).
6. *Rubus allegheniensis* Porter: This herb was not recorded on the quadrat, but it was fairly abundant on the transect. There were several patches of these plants, closely clustered together. These were, on the average, about three feet high.

The herb coverage here was pretty close to 100 per cent. The sod varied from two to three inches in thickness and was permeated by numerous roots. There was very little humus.

The ecotone between the Potentilla-Solidago-Rumex Associes and the Fagus-Acer Association was 11 meters wide and composed largely of maple, linden and ash. Between the Potentilla-Solidago-Rumex Associes and the Acer-Tilia-Sambucus Associes the ecotone was 42 meters wide and was composed mainly of *Tilia americana* L., *Sambucus canadensis* L., *Acer rubrum* L. and *Rubus allegheniensis* Porter.

Invertebrates

Quantitative

The invertebrates were studied by soil samples and net sweeps, the details of which have been discussed under "Methods." The counts of the fauna in the 0.1 square meter of soil samples were multiplied by ten for comparison with sweepings, since the writer proceeded on the bases that 48 sweeps were equivalent to one square meter of ground with 100 per cent herb coverage. Smith (1928) and Shakleford (1929) both used 50 sweep.

At best it is difficult to compare the number of invertebrates in 48 sweeps with those in one square meter of soil. The reason is that with the onset of fall and winter the herb stratum subsides with a consequent reduction in material available for sweeping. It is difficult to compensate accurately for this by reduced estimates of coverage. The reverse situation occurs in spring. Such conditions do not obtain in connection with the invertebrate population of the soil. These conditions make it difficult to make numerically accurate comparison between the invertebrate faunas of the two strata.

However, in making such a comparison it is noted that in the great majority of cases the fauna of the soil exceeded that of the sweeps, and in most cases the excess was great. Comparing the sweeps and the soil samples it was seen that only in July, August, September and October the invertebrates of the sweeps exceeded those of the soil. In all other months the fauna of the soil exceeded the fauna of the sweeps. The months in which invertebrates were collected from sweeps (in order of abundance) were as follows: October, November, July, June, August, September, May, December and April. No invertebrates were taken in sweeps during January, February and March. The invertebrate population of the herb stratum depends upon the seasonal presence and abundance of this predominantly annual vegetation. These in turn are no doubt dependent upon other factors.

Further quantitative discussion of the invertebrates will be done mainly on the basis of seasonal changes or aspection. The periods usually recognized are prevernal, vernal, aestival, serotinal, autumnal and hibernal.

In this study the periods of aspection have been divided, for purposes of discussion, as noted below. On account of differences in physical factors and the fauna of the several communities studied it was difficult to draw the lines of demarkation between the various seasonal changes for the community as a whole. Therefore, the seasonal periods as designated can hardly be any too accurate and should be interpreted as an approximation. The discussion of the data, as noted below, is based on approximately two week periods.

Autumnal period (September 30 to November 30): The work was started at this station on October 19, and the average number of specimens for this part of the month, per square meter, was 85 and the average number in the 48 sweeps was 120.5. The mean temperature from October 19 to the 31, was still fairly high: 56° in the soil, 68° on the surface and 67.65° in the air. The rainfall was 2.2 inches and the relative humidity 59 per cent.

From November 1 to the 15, the average number of invertebrates per square meter of soil was 167 and the average per 48 sweeps 86.7. An increase in soil fauna is noted, whereas the opposite is true of the sweeps. This finding seems to be in accord with the facts derived from the physical data. The temperature had dropped to the lower forties, whereas in October it was in the upper fifties and lower sixties. The ground was now perhaps cool enough and had sufficient moisture in the first three inches to cause the invertebrate migration back towards the surface rather than downward as was probably the case in October. Still another reason for the increase of the soil fauna is seen in the decrease of herbs. As the temperature continued to drop they moved down to take cover on the ground beneath the vegetation, and some also burrowed into the soil where the temperature was much higher.

From then on into the winter there was a gradual reduction of invertebrates found in the sweeps due to the loss of herb coverage and reduction in temperature. This also accounted for the decrease in sweep specimens during the first half of November.

From November 16 to the 30, there was a marked decrease in the number of invertebrate specimens from both sweeps and soil samples. The average number being forty for each square meter of soil and eighteen for the 48 sweeps. It seems that the decrease in fauna is due to differences in physical factors. All physical factors, except humidity, were lower for the last half than for the first half of November. The relative humidity was about 11 per cent higher. The rainfall, which was much lower, was 1.49 inches for the first half of November and only .45 inches for the last half. However, among the physical factors the reduction in temperature is the most probable cause of the decrease in invertebrates during the last half of November. They had moved down deeper into the soil where the temperature was higher.

Hiemal period (November 30 to March 15): There was a decrease in the fauna of both the soil and sweep samples during the first half of December. The temperature of the soil and surface had decreased somewhat but the temperature of the air showed a very marked decline. At the beginning of December there was little to sweep for most of the leaves had been shed by this time.

The latter half of December witnessed a further decline in the fauna of the soil as compared with the first half, and nothing was found in the sweeps. The temperature was lower for this period of time than it was for the first half of December. The rainfall was also less, but the humidity higher. The decrease in the number of soil invertebrates was probably due to the decreased temperatures. As it grew colder near the surface the invertebrates moved deeper into the soil to warmer regions.

During the first half of January the soil fauna increased over that of the last half of December. The temperature of the soil and air were a little higher, the rainfall slightly higher and the humidity lower.

The latter half of January witnessed a further rise in the number of invertebrates of the soil but nothing from sweeps. There was only a slight drop in temperature but apparently not enough to stop the increase in soil population started in the first half of January. The temperature of the soil was 1.71° lower and the surface .9° lower. The relative humidity was much lower for the last half of January than for the first half.

For the first half of February the invertebrates were a little less numerous than for the preceding period. The temperature of the soil and surface was slightly higher. The rainfall and relative humidity were higher, the latter much higher.

During the latter half of February the number of invertebrates was less than for the first half. The temperature of the soil and surface during the last half of February was only slightly lower than the

first half; the rainfall much higher and the relative humidity lower. During this period nothing was taken in sweeps.

The first half of March witnessed an increase in fauna over the two periods already discussed in February; in fact, the highest number of invertebrates per square meter of soil was collected since the last half of January which it equaled. Nothing was recorded from the sweeps. The mean temperatures of soil and surface were a little lower than for the last half of February, but the air temperature was slightly higher. The rainfall was much lower but the relative humidity much higher.

Prevernal period (March 15 to April 21): The number of invertebrates collected during the last half of March was but a few, the average per square meter of soil being ten and nothing from sweeps. There was only a slight rise in ground and surface temperatures, whereas the air temperature indicated a significant rise, about 10° higher. The relative humidity was about 6 per cent less and the rainfall only slightly higher.

From April 1 to the 15, the average number of soil invertebrates was 101.7 but nothing from the sweeps. For the first time since the first half of November, the soil and surface temperatures were as high as 40°. The air temperature was 38.66°; the rainfall 2.40 inches and the relative humidity 70 per cent.

Vernal period (April 21 to June 15): The last half of April brought a very marked increase in temperature readings: The ground was 48.65°; surface 50.40°, and the air 59.90°. The rainfall was less, 1.75 inches, and the relative humidity also less, 68 per cent. The number of invertebrates was much less than for the first half of April, 70 per square meter of soil. For the first time since the first half of December one specimen was collected in the sweeps.

During the first half of May there was a slight decrease in the number of invertebrates. The soil and surface temperatures were a little higher, but the air temperature was much lower. The rainfall was 1.21 inches and the relative humidity 84 per cent, the latter much higher than that during the last half of April. Nothing was taken in the sweeps.

For the last half of May the number of invertebrates of the soil increased over that of the last period, 103.3 per square meter of soil and 4.7 per 48 sweeps. The temperatures were in the first part of the sixties, the rainfall was 1.75 inches and the relative humidity 72.6 per cent.

For the first half of June the invertebrate fauna of the soil dropped low, averaging ten specimens per square meter of soil, whereas there was an increase in the number in sweeps, 19.5 specimens for each 48 sweeps. The temperature of the soil was now 66.69°, the surface 77.08°, and the air 81.59°. The rainfall was 2.50 inches and the relative humidity 68 per cent.

Estival period (June 15 to August 30): The number of invertebrates collected from the soil during the last half of June was thirty-five per square meter and eleven per 48 sweeps. This was an increase in soil and a decrease in sweeps as compared with the first half of June. During the last half of June there was a drop in all three temperature readings, soil, surface, and air; the drop in the soil temperature was marked. The rainfall was 2.75 inches, the relative humidity 68.5 per cent; these were practically the same as for the first half of this month.

For the first half of July nothing was taken in the soil samples but an average of twenty-seven specimens was taken in the sweeps. The soil temperature was 71.64°, the surface 78.35° and the air 84.20°. The rainfall was two inches and the relative humidity 58 per cent. The scarcity of moisture, made possible by high temperatures, was the determining factor in the scarcity of invertebrates. Seasonal changes might also be a probable factor.

The number of invertebrates was greater from the soil but less from sweeps for the last half of July than for the first half. But the number was still low. On a whole temperatures were greater, the rainfall was less but the relative humidity much higher. Seasonal changes and scarcity of moisture are factors in limiting the invertebrate fauna. The latter being the most probable cause.

For the first half of August the invertebrate fauna of the soil was still low, less than for the preceding period, but there was a slight increase in the number from sweeps. The temperature readings were beginning to drop a little. The rainfall was .7 inches, and the relative humidity 69 per cent.

The invertebrates from both soil and sweeps had markedly declined during the last half of August. All temperatures were less, but the rainfall and relative humidity were higher.

During July and August the extreme dry condition was the most important factor in limiting the number of soil invertebrates. Seasonal changes also constituted a possible limiting factor.

Serotinal period (August 30 to September 30): During the first ten days of September nothing was taken from the soil, but there was an increase in the number from the herbs, averaging twenty-seven per 48 sweeps. The temperature readings were much lower and the rainfall and relative humidity were also slightly lower than for August.

Out of twenty-one cases discussed above for comparison, it is noted that in six cases when the soil temperature decreased the number of soil organisms also decreased, and in four cases when the temperature increased the soil fauna likewise increased. On the contrary, in five cases when the temperature decreased the soil fauna increased and in six cases an increase in temperature brought a decrease in soil fauna.

It appears that the temperature is a very important physical factor affecting the movement of soil fauna, especially during the winter.

From November 1 to April 15, the colder period, the average number collected per square meter of soil was 76.25. The soil temperature during this

period of time ranged from 31.82° to 42.97°. From April 16 to September 10 plus the last half of October, the warmer period, the average number of soil fauna collected was 36.35 per square meter. During the latter period the soil temperature ranged from 48.65° to 77.42°. A much larger number was collected during the colder than the warmer period, even though they were about equal in length. The months listed in order of abundance of soil fauna were as follows: November, February, April, May, January, March, December, July, August and September.

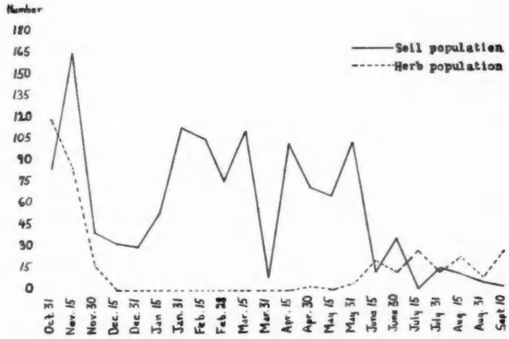

FIG. 6. Graphs showing the invertebrate population of the Herb and Soil strata of the Potentilla-Solidago-Rumex Associes (Station I). Counts based on number of specimens per square meter or per 48 sweeps. Graphs based upon collections covering approximately two-week periods.

Annotated List of Most Common Invertebrates

Oligochaeta

Diplocardia sp:—One specimen was taken in each of the following months: November, on December 11, February 13, in April and May. The soil temperature on December 11, was 37.4° and on February 13, 33.8°.

Lumbricus sp:—Two specimens were collected on November 2.

This associes, in the first three inches of soil, showed a very marked scarcity of earthworms; they were apparently not sufficient in numbers to have any marked influence upon the soil of the biotic community in which they live. In general the effect of earthworms in certain communities has been overestimated. Other burrowing forms such as ants were greater in numbers and in reaction than earthworms.

Araneida

Clubiona sp:—These spiders were collected as adults in November, on February 1 and 13, in July and August. On February 1, the temperature of the soil was 33.44°, that of the surface 32.9°. On February 13, the temperature of the soil was 33.8°, and that of the surface 32.3°. Those in August were taken in the herb stratum, otherwise they were taken from the soil.

Dictyna volucripes Keys:—This species of spider was quite abundant. Individuals were collected in November, on December 4, February 11, in April, June and September. The soil temperature on February 11, was 34.74° and that of the surface 32°. Those taken in December were immature. All were taken in the herb stratum, except one which was collected on February 11.

Anyphaena celer (Hentz):—This species was taken in the adult stage on January 18, in the soil stratum. The temperature of the soil on this date was 32.9° and that of the surface 28.4°. Other specimens belonging to this genus were collected from the soil in December, March and May. Those collected in the two latter months were immature.

Phidippus insolens (Hentz):—This spider was collected during July and August, all were in the adult stage and taken in the herb stratum.

Diplopoda

Polyzonium rosalbum Cope:—This species was taken on January 18; the ground temperature on this date was 32.9° and the surface was 28.4°. Williams and Hefner (1928) state that this species lives in rotten wood and soil just below it.

Chilopoda

Geophilus strigosus McNeill:—This centipede was taken on February 28, March 6, in April, May and August. On February 28, the ground temperature was 34.15° and on March 6, 30.74°. Williams and Hefner maintained that the habitats of this group include tunnels of boring insect larvae in rotten logs, deep crevices of rock-strewn or vegetable littered areas, and earthworms burrows in the soil.

Lithobius bilabiatus Wood:—This species was taken on February 13, and in May and June. On February 13, the ground temperature was 33.8°.

Linotenia fulva Sager:—This centipede was taken on February 21, and on this date the ground temperature was 33.44°.

Orthoptera

Conocephalus sp:—These specimens were collected during June, July and August. There were only four, one a nymph and the remainder adults.

Melanoplus femur-rubrum De Geer:—This species was collected on January 18, in the soil stratum. It was probably hibernating on the surface beneath the vegetation. On January 18, the temperature of the surface was 28.4°.

Gryllus assimilis (F.):—This species was taken on December 11, in the nymph stage. It was probably hibernating on the ground beneath the vegetation since it was collected in soil samples. On December 11, the temperature of the surface was 34.70°.

Hemiptera

Lygus oblineatus (Say):—These insects were collected in the sweeps only. They were found in both the nymph and adult stage, but mostly in the latter. They were limited in the collections to the summer season.

Cymus angustatus Stal:—This species was taken in June, July and September, in sweeps only, all in the adult stage.

Phlegyas abbreviatus Uhler:—About thirteen of these Hemiptera were taken, some in June, July, August and September; all in the adult stage and in sweeps.

Mormidea lugens Fab.:—This species was collected in sweeps during July, August and September.

The four species of Hemiptera discussed live mainly on vegetation. It should be noted that none of the above Hemiptera were taken during the winter.

Homoptera

Driotura gammaroides (Van D.):—This species was collected in sweeps as nymphs in November, and as adults in May. They probably hibernate as nymphs.

Philaenus leucophthalmus (L.):—This insect was collected in sweeps in the adult stage in July, August and September. It was abundant. It is usually found on herbs, shrubs and trees.

Coleoptera

Harpalus sp:—Several adults of this genus were collected in the soil samples in November, on January 4, February 21, in March and May. On January 4 the ground temperature was 33.26° and the surface temperature 29°. On February 21, the ground temperature was 33.44° and the surface 32°.

Acupalpus hydropicus (Lec.):—This species was limited to a few specimens in the adult stage collected from the soil on February 13 and 21. On February 13, the temperature of the surface was 32.36° and the ground temperature 33.8°. On February 21, the temperature was 32° on the surface, and 33.44° in the ground.

Stonolophus fuscatus Deg.:—All were adults and collected in February from the soil.

Agriotes sp., *Melanotus* sp., and *Ludius* sp.:—These three genera were collected as larvae in small numbers. In the larval stage they are commonly known as wireworms. Agriotes was taken on October 19, Ludius on October 19 and 26, and Melanotus on November 13 and February 1. The ground temperature on February 1, was 33.44°.

Hippodamia parenthesis Say:—This is one of the lady-bug beetles. A few adults were taken in sweeps during August. These insects are considered very beneficial, since in both the larval and adult stage they are predaceous, especialy upon injurious insects.

Anaedus brunneus Ziegl:—One adult was taken in November and one in April from soil samples. Comstock maintained that this family occurs chiefly in dry and warm regions and that while we have comparatively few species in the northeastern United States there are many in the southwest.

Paria canella Fab:—This species was abundant and was collected in every month except October and December. From November until the end of May all were taken from soil samples. From June to September 10, the date this study was discontinued, all were taken in sweeps. These beetles were taken at such low temperatures as follows: On January 11, the temperature of the surface was 32° and the ground 35.42°. On February 11, the surface temperature was 32° and the ground 34.7°. On March 6, the surface was 30.74° and the ground 31.46°. On March 28, the surface was 32.0° and the ground 33.0°. All specimens were collected in the adult stage.

Graphops sp:—These bettles were found in the soil during November, on January 4, February 28, and in April and May. They were fairly abundant, both larvae and adults, but mostly the latter. Most of the larvae were taken in April. On January 4, the temperature of the surface was 29.12° and the ground 33.26°. On February 28, the temperature of the surface was 32.0° and the ground 34.10°.

Nodonota sp:—These insects were taken from the soil in the larval stage during November, on February 1, and March 13. On June 3, three adults were taken in sweeps. The temperature of the surface on February 1, was 32.90° and the ground 33.44°. On March 13, the temperature of the surface was 32° and the ground temperature 33.44°.

Galerucella cribrata Lec:—This species was fairly abundant. All were in the adult stage and collected in sweeps during July and August.

Zygogramma suturalis Fab:—These beetles were taken as adults in soil and sweeps in June and July.

Brachyrhinus sulcatus Fab:—This species was collected in sweeps and soil in the adult stage. They were found on March 6, in June and September. On March 6, the temperature of the surface was 31.46° and the ground was 30.74°.

Lepidoptera

Phalaenidae sp:—These specimens were taken from soil samples in the larval stage during the winter and mostly from sweeps during the summer. Many were found in the flowers of golden rods. On February 13, some were collected from the soil. On this date the temperature of the surface was 32.36° and the ground 33.8°. On February 28, one was collected from the soil with a surface temperature of 32° and a ground temperature of 34.16°.

Olethreutidae:—Some of these specimens were collected every month at this station except January and September. On October 19, 233 larvae were collected in 48 sweeps. They were found mostly in the flowers of golden rods during the summer. Some of these larvae were collected at such low temperatures as follows: On February 21, the surface temperature was 32°, the ground temperature 33.44°. On March 13, the surface temperature was 32° and the ground temperature 33.4°.

Diptera

Minettia lupulina (F.):—Several specimens were collected in sweeps on September 10.

Hymenoptera

Lasius niger (L.) var. female:—This species of ant was collected in soil samples in October, November and on March 13. On the latter date the surface temperature was 32° and the ground temperature 33.4°.

Lasius niger var. *americana* Emery, female:—Several specimens were collected in the soil on May 16

Lasius umbratus mixtus var. *amphidicola* (Walsh). —This species was collected in the soil in April and May.

Myrmica sp:—These ants were collected from the soil in October, on January 27, February 21, in June and July. On January 27, about twenty of these ants were collected with a surface temperature of 30.92° and a ground temperature of 32.36°. On February 21, some were collected with a surface temperature of 32° and a ground temperature of 33.44°.

Ants, no doubt on account of their large numbers, their highly developed social organization, their intense activity and feeding habits, exert a very great influence upon the biotic community in which they live. They are, therefore, coactors in no small capacity upon their biotic community and have important reactions on the soil.

Vespoidea:—These larvae were collected in soil samples on February 28. On this date the surface temperature was 32° and the ground temperature 33°.

The number of species found among the invertebrate groups in the two strata were as follows:

	Soil	*Sweeps*	*Totals*
Coleoptera	9	10	19
Hemiptera	5	8	13
Araneida	7	4	11
Hymenoptera	4	5	9
Chilopoda	2	2	4
Diplopoda	3	0	3
Homoptera	0	3	3
Orthoptera	2	1	3
Diptera	0	2	2
Isopoda	1	0	1
	33	35	68

Lepidoptera were fairly abundant but as they were in the larval stage none were determined as to species.

SOLIDAGO-AGROSTIS-DAUCUS ASSOCIES (STATION II)

This associes was adjacent to and directly south of the Quercus-Carya Associes (Station III). It was most distant from houses but like the others was cut across by dirt roads. One road extended across this associes from east to west in a somewhat winding fashion. This road gave off two other branches within the vicinity of this station, one going north and the other south. In these roads the red top and panic grasses thrive best. Much of the collecting was done close to these roads and sometimes directly in the roads.

This community, now in the developmental stage, appears to have been a beech-maple climax community which was subsequently cut. This opinion is based on logs and stumps of beech and maple as well as seedlings of same. There were no large standing trees in this community. The sod varied from two to three inches in thickness. There was little humus. The herb coverage was not continuous but was interrupted by shrubs. However, in such places where the herbs occurred they were very thick and the estimated coverage of the latter was about 75 per cent.

In taking the sweep samples at the stations located in the woods the herbs as well as the low-shrubs were included. It was necessary to include the low-

TABLE 1. Predominants of the Potentilla-Solidago Rumex Associes (Station I).

Species	Total Number	Number in Soil	Number in Sweeps	Average Number and Average Per Cent Per Meter Square or Per 48 Sweeps: Soil Number	Soil Per Cent	Sweeps Number	Sweeps Per Cent	Prevernal Period (March 15 to April 21)	Vernal Period (April 21 to June 15)	Estival Period (June 15 to August 30)	Serotinal Period (August 30 to September 30)	Autumnal Period (September 30 to November 30)	Hiemal Period (November 30 to March 15)
Olethreutidae	392	120	272	2.55	4.08	5.79	33.05	10	......	......	......	362	20
Graphops sp.	350	350	......	7.46	11.90	......	......	200	30	......	......	60	60
Myrmica sp.	244	240	4	5.12	8.16	.08	.49	......	......	14	......	10	220
Coleophora sp.	226	10	216	.21	.34	4.60	26.24	......	......	......	......	225	1
Paria canella Fab.	227	180	47	3.83	6.12	1.00	5.71	20	26	25	6	70	80
Geophilus strigosus McNeill	130	90	40	1.92	3.06	.85	4.86	10	70	10	......	......	40
Phalaenidae	90	80	10	1.70	2.72	.21	1.21	......	10	11	......	37	32
Galerucella cribrata Lec.	36	......	36	......	......	.77	4.37	......	......	36	......	......	......
Philaenus leucophthalmus (L)	24	......	24	......	......	.51	2.92	......	......	19	5	......	......
Dictyna volucripes Keys	32	10	22	.21	.34	.47	2.67	......	11	......	3	5	13
Lygus oblineatus Say	28	......	28	......	......	.59	3.40	......	......	11	9	8	......
Cymus angustatus Stal	13	......	13	......	......	.28	1.58	......	9	2	2	......	......
Phlegyas abbreviatus Uhler	13	......	13	......	......	.28	1.58	......	2	7	4	......	......
All other species	1958	1860	98	39.57	63.24	2.08	11.91	120	426	187	25	510	690
TOTALS	3763	2940	823	62.5	100	17.51	100	300	584	322	54	1287	1156

shrubs on account of the scarcity of the herbs. The herbs were more abundant at this station than any of the others located in the woods.

Vegetation

The dominants here were *Solidago canadensis* L., 25.9 per cent; *Agrostis alba* L., 20.2 per cent; and *Daucus carota* L., 12.7 per cent. These three dominants ranked high in both the quadrat and transect counts. *Panicum implicatum* Scribn. ranked 11.7 per cent in the quadrat counts but only 2 per cent in the transect which hardly justifies its inclusion as a dominant.

The map (Fig. 1) shows that the area studied was limited in vegetation of the same kind which surrounds this station. In fact, no other part of the area studied contained vegetation similar to that found at this station.

The subdominants were as follows:

Panicum implicatum, Scribn., 11.7 per cent;
Viola papilonacea Pursh, 8.4 per cent;
Lactua sp., 7.6 per cent.

The first two subdominants were recorded in the quadrat and the transect, but the last one was recorded only in the transect. Other subdominants listed in the transect but not in the quadrat were as follows:

Acer saccharum Marsh, seventy-nine seedlings along a transect of 109 meters;
Acer rubrum L., sixty-four seedlings;
Quercus rubra L., fifty-four seedlings;
Rubus allegheniensis Porter, thirty-nine and
Fagus grandifolia Ehrh., twenty-four seedlings.

The ecotone between the Solidago-Agrostis-Daucus Associes and the Quercus-Carya Associes was composed mainly of the following plants:

Carya ovata (Mill) K. Koch,
Quercus rubra L.,
Panicum implicatum Scribn and
Ulmus americana L.

The ecotone was twenty-two meters wide.

Invertebrates

Quantitative

Comparing the average number of specimens found in one square meter of soil with the average number found in 48 sweeps, it is noted in the great majority of cases the number of soil specimens exceeded those of the sweeps. In most cases the excess was great. The average number of specimens found in the sweeps exceeded the average number in the soil only in July, August and September. The months in which invertebrates were collected from sweeps (in order of abundance) were as follows: August, November, July, June, September and May. From December to May 15, nothing was found in the sweeps.

Autumnal period (September 30 to November 30): The work was started at this station on November 9. Between this date and November 16, two collections were made with an average of eighty-five specimens per square meter of soil and twenty-seven per 48 sweeps. The mean temperature for this period was as follows: soil 55.58°, surface 51.35° and air 56.57°. The rainfall was .09 inches and the relative humidity 54.5 per cent.

From November 17 to the 30, the invertebrates increased markedly over the preceding period. The temperature had dropped sharply, between ten and fifteen degrees; the relative humidity had increased up to 70.5 per cent, the rainfall had only a slight increase. The increase in the invertebrates was no doubt due to the sharp fall in the temperature which caused the ground to become cooler and hence the retention of more moisture.

Hiemal period (November 30 to March 15): From December 1 to the 15, the number of invertebrates decreased sharply in the soil samples and nothing was taken in the sweeps. The decrease in temperature was only about 2°, but perhaps responsible for the further reduction in invertebrates.

From December 16 to the 31, there was a further decrease in soil fauna, but nothing from sweeps. The decrease in temperature was great, between 7° and 15°. The soil temperature was 32.9° and the air 24.80°.

Since nothing was found in the sweeps from December through May no further remarks will be made about the sweeps until the month of May is discussed.

From January 1 to the 14, there was an increase in soil fauna. There was also an increase in the temperature of soil and surface, between 1.53° and 2.52°. The relative humidity had increased slightly.

From January 15 to the 31, the fauna of the soil decreased. The temperature of the soil and surface dropped slightly, about 1° for the soil and less than 1° for the surface.

From February 1 to the 14, the increase in the soil fauna was great. The temperature of the soil and surface increased slightly, around 1°. But the increase in the air temperature was about 5°. The relative humidity and rainfall remained practically the same.

From February 15 to the 28, there was a great slump in the number of invertebrates. There was a slight drop in temperature in the soil and surface. The temperature drop averaged about 3°. The relative humidity was higher.

The first half of March witnessed a very large increase in the soil fauna, the largest of any period so far, 320 per square meter of soil. The temperature increase the first half of March averaged 2.61° for the three strata. The relative humidity was much higher, being 94.5 per cent.

Prevernal period (March 15 to April 21): During the latter half of March no specimens were taken. One collection was made. The temperature of the surface and air increased between 2° and 3°, but the soil indicated a slight decrease, about 1°. The relative humidity had dropped a little as compared with the preceding period.

The first half of April received an increase in the number of soil invertebrates, seventy per square meter. The temperature of the soil greatly increased. The rainfall was the heaviest so far, 2.16 inches; and the relative humidity 78 per cent, the latter a decrease over the preceding period. The greatest change in physical factors of this period over the preceding one was temperature, the rise varied between 3° and 9° between the three strata.

Vernal period (April 21 to June 15): During the latter half of April nothing was collected. The temperature made a very marked increase over the preceding period. The increase was about 7°, 15°, and 21° in soil, surface and air respectively. The relative humidity was 58.2.

The first half of May received an increase in soil fauna, twenty specimens per square meter. The soil temperature was still increasing. The relative humidity was 74 per cent and the rainfall 1.07 inches.

The latter half of May the fauna of the soil was twice as great as for the first half. The temperature was considerably higher, it had reached the sixties. The relative humidity was lower, but the rainfall was higher. For the first time since the latter half of November specimens were taken in sweeps, seven per 48 sweeps.

From June 1 to the 15, the number of invertebrates greatly increased, 260 per square meter of soil and thirty-four per 48 sweeps. During this period the temperature reached its peak, from then on there was a gradual falling off. The relative humidity and rainfall were greater than for the preceding period.

Estival period (June 15 to August 30): For the latter half of June the soil fauna was zero, the sweeps averaged twenty-eight specimens per 48 sweeps. The temperature was much reduced and the relative humidity was lower. But the rainfall was still very heavy, 4.70 inches. Although there was an appreciable drop in temperature, it was difficult to account for such negative results in soil fauna on the basis of temperature alone.

The first half of July the fauna of the soil averaged five specimens per square meter and thirty-one per 48 sweeps. The temperature also increased a little; the rainfall was 1.75 inches, and the relative humidity 69.4 per cent.

During the latter half of July there was a good increase in specimens from sweeps, but a slight decrease in soil fauna. The temperature and relative humidity also increased, but there was a slight drop in the amount of rainfall.

From August 1 to the 15, the soil invertebrates increased but the sweeps showed a marked decrease. The temperature, relative humidity and rainfall were only slightly lower.

For the latter half of August the soil fauna remained the same but the increase was great from sweeps. The temperature was lower, the relative humidity and rainfall were higher.

Serotinal period (August 30 to September 30): During the first ten days of September there was an increase in soil fauna but a marked decrease in sweeps. The temperature had undergone a considerable drop. The temperatures of the three strata were as follows: soil 61.59°, surface 51.28° and air 62.29°. The relative humidity was also less, 74.4 per cent; the rainfall was 1.15 inches.

From a study of the twenty periods or cases compared above in every case, except six, with each increase or decrease in soil temperature there was an increase or decrease in soil fauna.

In this associes temperature seems to be the most potent factor affecting the vertical migration of soil invertebrates.

Soil fauna in this associes is more abundant in the first three inches during the colder than the warmer months. The average number collected per square meter of soil from November 17 to April 15, the colder period, was 99.8; and from April 16 to September 10, plus the period of time from November 9 to the 16, the warmer period, was 44.8. The number of specimens during the colder period was far in excess of the number during the warmer period. During the colder period the soil temperature ranged from 32.90° to 42.26°. During the warmer period it ranged from 49.01° to 73.3°. The months listed, in order of abundance, as per number of soil invertebrates were as follows: March, November, June, February, January, December, April, May, September, August and July.

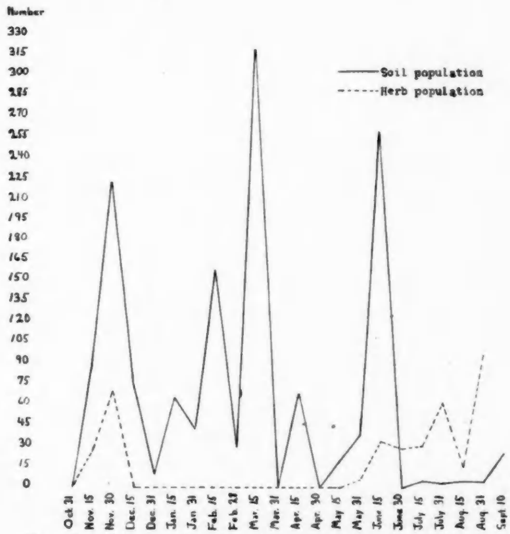

FIG. 7. Graphs showing the invertebrate population of the Herb and Soil strata of the Solidago-Agrostis-Daucus Associes (Station II). Counts based on number of specimens per square meter or per 48 sweeps. Graphs based upon collections covering approximately two-week periods.

Annotated List of Most Common Invertebrates

Oligochaeta

Lumbricus sp:—These worms were collected in November, on December 29, January 31 and February 26, only five. The ground temperature on Decem-

ber 29, was 32.90°, on January 31, 34.88° and on February 26, 33.8°.

Diplocardia sp:—These specimen were collected in November, on February 11, in April, May and June. On February 11, the ground temperature was 34.7°.

Pulmonata

Ventridens intertexta (W. G. Binney):—Two specimens of this snail were collected from the soil stratum, one on November 9, and one on April 15.

Diplopoda

Polydesmus moniliaris Koch:—This species was collected from the soil in the immature stage in November and in the adult stage in December and on March 11. On the latter date the ground temperature was 33.8°.

Chilopoda

Geophilus strigosus McNeill:—These centipedes were taken in December, February, on March 11, in April and May. All were in the adult stage. On March 11, the ground temperature was 33.8°.

Orthoptera

Melanoplus sp:—From July 17 to September 10, about 83 adults were collected from sweeps. The great majority of these insects were collected in August. On August 21, forty-five were collected and on August 28, twenty-two were collected.

Conocephalus sp:—These specimens were taken in sweeps in August, some were nymphs and some adults.

Hemiptera

Phlegyas abreviatus Uhler:—This species was taken in the sweeps only. They were collected from June 13 to September 10, about 54 specimens, all in the adult stage.

Cymus angustatus Stal:—This species was abundant, all were adults and collected in sweeps. They were taken in June, July, August and September.

Orthaea basalis Dall:—Eleven specimens of this species were taken in sweeps on November 9, all were in the adult stage.

Corythucha marmorata Uhl:—This species was collected in July, August and November, from both sweeps and soil. All were adults.

Euschistus euchistoides (Voll.):—This insect was collected in sweeps in the adult stage in July and August.

Mormidea lugens Fab:—These insects were collected in Ju'y, August and September, all from sweeps and in the adult stage.

Miridae:—On July 17 and the 31, about fifty-three specimens were collected from sweeps, mostly nymphs but some adults.

Lygus oblineatus Say:—This species was limited to sweeps. They were collected in June, July, August, September and November. All were in the adult stage.

Homoptera

Philaenus leucophthalmus (L.):—This species was collected in July and August; all were taken in sweeps and all were adults.

Coleoptera

Paria canella Fab:—Numerous adults of this species were collected both in sweeps and the soil stratum but largely from the former. During the winter months, they were collected only in the soil and during the summer only in the sweeps. They probably hibernate in the ground. Some were collected on March 11, with a surface temperature of 41° and a ground temperature of 33.8°.

Podabrus sp:—These beetles were collected in November, January and March, both in the adult and the larval stage. The larvae were confined to soil samples. Adults were taken in soil and sweeps.

Graphops sp:—These insects were collected during February, March and April, all were taken from the soil.

Photinus marginellus Lec.:—This species was taken in June and July in the adult stage. They were found only in sweeps.

Harpalus sp:—These beetles were limited to the soil samples. They were collected in November, December, January, March and April. All were adults.

Lepidoptera

Phalaenidae:—These larvae were collected in June, July, August and November. They were taken in sweeps in all months, except November.

Coleophora sp:—These specimens were taken in very large numbers, all in November and all in the larval stage. They were collected in sweeps.

Hymenoptera

Formica fusca var. *subsercea* Say:—This species of ant was collected in July and August. They were limited to sweeps.

Crematogaster lineolata (Say) var. *near cerasi* (Fitch):—This species was taken on June 13, in sweeps. They were abundant.

Formica exsectoides Forel:—This ant, like the above, was also taken in sweeps, on June 13, and they were fairly abundant.

The number of species found among the invertebrate groups in the two strata were as follows:

	Soil	*Sweeps*	*Totals*
Coleoptera	10	17	27
Hemiptera	7	14	21
Araneida	4	9	13
Hymenoptera	9	8	17
Diplopoda	3	4	7
Homoptera	0	4	4
Diptera	0	3	3
Chilopoda	2	0	2
Pulmonata	1	0	1
Orthoptera	0	1	1
	36	60	96

TABLE 2. Predominants of the Solidago-Agrostis-Daucus Associes (Station II).

Species	Total Number	Number in Soil	Number in Sweeps	Average Number and Average Per Cent Per Meter Square or Per 48 Sweeps				Prevernal Period (March 15 to April 21)	Vernal Period (April 21 to June 15)	Estival Period (June 15 to August 30)	Serotinal Period (August 30 to September 30)	Autumnal Period (September 30 to November 30)	Hiemal Period (November 30 to March 15)
				Soil		Sweeps							
				Number	Per Cent	Number	Per Cent						
Myrmica sp.	536	530	6	12.61	17.97	.14	.70		512	4		20	
Harpalus sp.	190	190		4.52	6.44			20					170
Coleophora sp.	164		164			3.90	19.02					129	35
Paria canella Fab.	147	110	37	2.62	3.73	.88	4.29		16	21		30	80
Geophilus strigosus McNeill	140	140		3.33	4.75			10	50				80
Cymus angustatus Stal.	126		126			3.00	14.62		3	120	3		
Podabrus sp.	111	110	1	2.62	3.73	.02	.12					10	101
Melanoplus sp.	81		81			1.93	9.40			67	14		
Graphops sp.	80	80		1.90	2.71			40					40
Polydesmus moniliaris Koch.	71	70	1	1.67	2.47	.02	.12					21	50
Corythuca marmorata Uhl.	71	30	41	.71	1.02	.98	4.76			41			30
Miridae	51		51			1.21	5.92			51			
Phaleanidae	11		11			.26	1.28			8		3	
Phlegyas abbreviatus Uhler	54		54			1.28	6.26		10	39	5		
Euschistus euchistoides (Voll.)	47	20	27	.48	.68	.64	3.13		10	37			
Lygus oblineatus Say	28	10	18	.24	.34	.42	2.09		2	6	10		10
Photinus marginellus Lec.	18		18			.42	2.09			18			
All other species	1885	1660	225	39.51	56.27	5.35	26.10	70	146	153	70	253	1193
TOTALS	3811	2950	861	70.2	100.	20.45	100.	140	749	565	102	466	1789

QUERCUS-CARYA ASSOCIES (STATION III)

This associes was located between the Acer-Tilia-Sambucus Associes (Station IV) and the Solidago-Agrostis-Daucus Associes (Station II) and adjacent to these and to the Potentilla-Solidago-Rumex Associes (Station I). This associes had a higher elevation than any of the other communities studied and hence less moisture. It was cut across by a road in a southeast direction which ran deeper into the forest beyond the vicinity of this community. This road sent out obscure tributaries as it passed through the Quercus-Carya Associes. All such roads were used principally for getting wood, sometimes by hunters, picknickers, etc. Much of the collecting was done within eight or ten meters of this road. The sod varied from two to three inches in thickness and was permeated by numerous roots. The humus was about one inch deep and the herb coverage about 35 per cent.

Vegetation

The dominants here were *Carya ovata* (Mill) K. Koch and *Quercus rubrum* L. Of the first named dominant, along a transect of 156 meters, there were 187 seedlings; seven trees between two and four inches in diameter; eleven between four and eight inches and nine over eight inches in diameter. Of the last named dominant there were 167 seedlings; one tree between two and four inches in diameter; five between four and eight inches and one over eight inches in diameter.

No other part of the area seemed to have vegetation similar to this associes.

The subdominants were as follows:

Populus tremuloides, Michx, 147 seedling; *Acer rubrum* L., seventy-one seedlings, two trees between two and four inches in diameter, one between 4 and 8 inches and one over 8 inches in diameter;

Fagus grandifolia, Ehrh., thirty-three seedlings.

Two other subdominants based exclusively on quadrat counts were Erythronium sp., 39 per cent and *Maianthemum canadense* Desf. 27.7 per cent.

The ecotone between the Quercus-Carya Associes and the Acer-Tilia-Sambucus Associes was largely *Acer rubrum* L., *Quercus rubrum* L., *Fraxinus americana* L. and Vita sp.

Invertebrates

Quantitative

Comparing the relative abundance of soil and sweep specimens it might be noted from Figure 8 that the soil specimens usually exceeded those of the sweeps and in most cases the excess was tremendous. Only two specimens were taken in sweeps from November 15 to December 15, and from December 15, through April nothing was collected. One specimen was taken between May 1 and the 15; after the latter date the increase from sweeps became appreciable. The sweep specimens exceeded those of the soil only in September, and here the excess was slight. The months in which specimens were collected through sweeps, in order of abundance, were as follows: July, September, August, June, November, May and December.

Autumnal period (September 30 to November 30): Collecting was begun at this station on October 30.

Between the latter date and November 15, the fauna from soil and sweeps was low, averaging five specimens for one square meter of soil and 6.5 for 48 sweeps. At this time the temperature had fallen to the middle forties. The relative humidity was 72.5 per cent and the rainfall 1.51 inches.

The last half of November brought an increase in soil fauna but a decrease in sweep specimens. The temperature had a slight decrease; the relative humidity a slight increase.

Hiemal period (November 30 to March 30): For the first half of December the soil fauna had more than doubled that of the preceding period; the sweep specimens had increased slightly. The temperature had decreased, the relative humidity increased.

From December 16 to the 31, the soil fauna had decreased and nothing was found in the sweeps. The temperature had greatly decreased, the soil, surface and air were 33.8°, 28.40° and 24.8° respectively. The relative humidity was 88 per cent and the rainfall .30 inches.

From December 15, through April nothing was taken in the sweeps, hence no further reference will be made of sweep specimens until the month of May is reached in the discussion.

The first half of January received a decrease in soil fauna. The temperature of the soil and surface increased a little while the air decreased markedly. The relative humidity was 76, a decrease. The rainfall was very light.

The last half of January brought an increase in the soil invertebrates. The temperature of the soil and surface was only slightly less than the preceding period, but the air temperature was very much higher. The relative humidity was also higher.

The first half of February brought a very marked increase in soil funa, the highest number so far, 105 per square meter. The temperature and humidity had increased.

During the latter half of February the soil specimens decreased but the temperature and relative humidity had also decreased.

From March 1 to the 15, the number of invertebrates were greatly reduced. The temperature of all three strata was only a little less than the preceding period. The relative humidity was higher.

Prevernal period (March 15 to April 21): During the latter half of March nothing was found in the soil. Only one collection was made. The temperature of the soil and surface was only slightly higher, the air temperature was about 8° higher. The humidity was much higher, 98 per cent.

During the first half of April the soil fauna increased. The temperature of the soil and surface was much higher, the air slightly higher. The relative humidity was 84 per cent and the rainfall 2.16 inches.

Vernal period (April 21 to June 16): During the last half of April the soil fauna decreased. The temperature was markedly higher but the relative humidity much lower, 59 per cent.

During the first half of May the soil fauna was a little less than for the preceding period and one specimen was taken in the sweeps. The temperature for all three strata was 49°. The relative humidity was 87.5 per cent.

For the last half of May the fauna of the soil and sweeps increased. The temperature increased greatly, it ranged from 61° to 73° between the three strata. The humidity was 65.7 per cent.

The first half of June the soil fauna decreased while the sweeps increased. The temperature was higher. The rainfall was 4.12 inches and the relative humidity 67 per cent.

Estival period (June 16 to August 30): From June 16 to the 30, the number of soil invertebrates remained about the same while the sweep specimens were less.

During the first half of July the fauna of both the soil and sweeps increased. The temperatures of all three strata also increased; the rainfall was less but the humidity practically unchanged.

For the last half of July the soil fauna was much reduced, whereas there was an increase in the sweeps. The temperatures were higher; the humidity was a little greater than during the preceding period. The temperature reached its peak here, it then took a slow decline.

For the first half of August the invertebrates increased from the soil but decreased from sweeps. The temperature was also less but the humidity was greater.

The last half of August brought an increase over the preceding period from sweeps but a decrease from soil samples. The temperature was a little lower. The relative humidity was about the same but the rainfall was greater.

Serontinal period (August 30 to September 30): During the first ten days of September the fauna of the soil remained the same while the sweeps increased. The temperature dropped about 7°. The relative humidity and the rainfall were less than for the preceding period.

In the twenty cases discussed above for comparison in all cases, except eleven, with each increase or decrease in soil temperature there was also an increase or decrease in the soil fauna. In one case, when the temperature changed the number of invertebrates remained the same. The number collected during the colder period exceeded the number taken during the warmer period. From November 15 to April 15, the colder period, an average of 48.5 specimens was collected per square meter of soil; whereas from April 16 to September 10, plus the first half of November, the warmer period, an average of 20.8 specimens was collected. A larger number was taken during the colder than the warmer period. The temperature of the soil during the colder period ranged from 31.93° to 43.12°. During the warmer period it ranged from 46.40° to 72.77°. The months listed, in order of abundance, as per number of soil invertebrates were as follows: February, December, April, January, June, May, July, November, March, August and September.

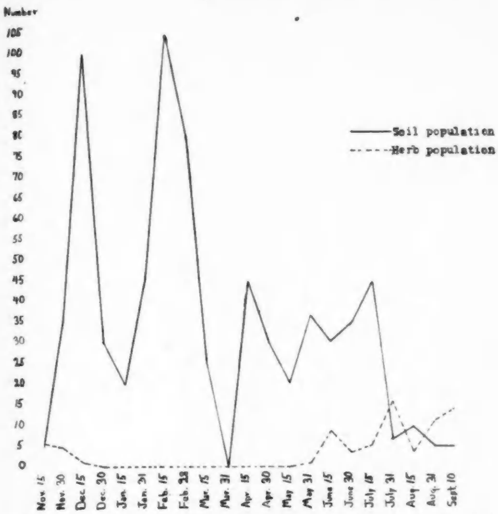

FIG. 8. Graphs showing the invertebrate population of the Herb and Soil strata of the Quercus-Carya Associes (Station III). Counts based on number of specimens per square meter or per 48 sweeps. Graphs based upon collections covering approximately two-week periods.

Annotated List of Most Common Invertebrates

Oligochaeta

Lumbricus sp:—These earthworms were collected on February 11, in March, April, May, June and July. On February 11, the ground temperature was 33.8°.

Diplopoda

Polyzonium rosalbum Cope:—This millipede was taken in soil samples in December, on February 20 and 26, in March and June. On February 20 and 26, the ground temperature was 33.8°.

Chilopoda

Geophilus strigosus McNeill:—This centipede was collected from soil samples on January 31, February 10, 11 and 20, in April, May and July. They were fairly abundant. On January 31, the ground temperature was 34.1° and on February 11 and 20, it was 33.8°.

Homoptera

Philaenus leucophthalmus (L.):—This species was collected in sweeps in the adult stage during July, August and November.

Coleoptera

Cantharis sp:—These adults were collected in sweeps during June and July.

Agriotes sp., *Melanotus* sp., and *Ludius* sp:—All specimens of these genera were wireworms and collected from the soil. Agriotes were few and taken in January. Melanotus was found on February 20 and 26, in April, August, and on December 14 and 29. Ludius was collected on January 31, February 20, in March, April, May and November. On February 20 and 26, and December 29, the ground temperature was 33.8°, and on December 14, it was 36.50°.

Paria canella Fab:—This beetle was collected in the adult stage on January 22, in May and September. In January it was collected from the soil, in May and September from sweeps. On January 22, the ground temperature was 33.8°.

Diptera

Bibio longipennis Lw:—This species was collected in sweeps in June, November and October. All were adults.

Sciara sp:—These larvae were collected from the soil on January 22, February 11 and 26, in March and November. On January 22, February 11 and 26, the ground temperature was 33.8°.

Dichomeris liguelella Hbn:—This species was collected during July and September; all were adults and taken in sweeps.

Hymenoptera

Myrmica sp:—These ants were collected on February 11 and 20, in May and June. Some were taken from sweeps and some from soil samples.

The number of species found among the invertebrate groups in the two strata were as follows:

	Soil	*Sweeps*	*Totals*
Coleoptera	6	8	14
Chilopoda	7	0	7
Hemiptera	2	5	7
Hymenoptera	3	4	7
Araneida	3	3	6
Lepidoptera	1	2	3
Diplopoda	2	0	2
Diptera	0	2	2
Homoptera	0	1	1
Isopoda	1	0	1
Neuroptera	1	0	1
	26	25	51

ACER-TILIA-SAMBUCUS ASSOCIES (STATION IV)

This associes was adjacent to the Potentilla-Solidago-Rumex Associes, Fagus-Acer Association and the Quercus-Carya Associes but nearest the former, as the map shows. This associes had the lowest elevation of all communities studied and, of course, held water longer. Much of the collecting at this station was done within fifty meters of the field in which Station I was located. Most of the collecting was done near a small unfinished cabin used by some of the children in the neighborhood as a playhouse. Many of the trees, varying from two to four inches in diameter, had been cut recently and presumably some were used in the erection of the cabin. The number of cut trees far exceeded the number used for construction of the cabin; some of the trees were undoubtedly used for firewood and other purposes. The sod here varied from two to three inches in thickness and was permeated by numerous roots. There was little humus.

TABLE 3. Predominants of the Quercus-Carya Associes (Station III).

Species	Total Number	Number in Soil	Number in Sweeps	Average Number and Average Per Cent Per Meter Square or Per 48 Sweeps				Prevernal Period (March 15 to April 21)	Vernal Period (April 21 to June 15)	Estival Period (June 15 to August 30)	Serotinal Period (August 30 to September 30)	Autumnal Period (September 30 to November 30)	Hiemal Period (November 30 to March 15)
				Soil		Sweeps							
				Number	Per Cent	Number	Per Cent						
Geophilus strigosus McNeill	140	140		3.33	10.21			20	60	10			50
Polyzonium rosalbum Cope	120	120		2.86	8.75					50			70
Lumbricus sp.	110	110		2.62	8.02				70	20			20
Myrmica sp.	79	70	9	1.67	5.10	.21	5.59		34	5			40
Sciara sp.	70	70		1.67	5.10							10	60
Ludius sp.	90	90		2.14	6.56			10	20			10	50
Melanotus sp.	81	80	1	1.90	5.83	.02	.62	10		21			50
Anaedus brunneus Ziegl.	62	60	2	1.43	4.37	.05	1.24		10	2			50
Phyllophaga sp.	42	40	2	.95	2.92	.05	1.24		10	22	10		
Helodrilus sp.	30	30		.71	2.19								30
Acupalpus hydropicus (Lec.)	30	30		.71	2.19							30	
Pardosa sp.	24	20	4	.48	1.46	.09	2.48	10		4			10
Dichomeris ligulella Hbn.	20		20			.48	12.42			17	3		
Porcellio rathkei Brandt	20	20		.48	1.46								20
Paria canella Fab.	18	10	8	.24	.73	.19	4.97		1		7		10
All other species	595	480	115	11.42	34.99	2.74	71.42	60	88	154	18	44	231
TOTALS	1531	1370	161	32.61	100.	3.83	100.	110	293	305	38	94	691

One of the old residents of the community informed the writer that a fire occurred here about a year before this work was started. It appeared that the fire was actually not quite as recent as that, but occurred perhaps two or three years ago.

Vegetation

The dominants along a transect of fifty-one meters were *Acer rubrum* L.: seedlings forty, trees two inches or over in diameter one, four inches or over in diameter four; *Tilia americana* L.: seedlings thirty-two, trees two inches or over in diameter seven, four inches or over in diameter eleven, eight inches or over in diameter five; *Sambucus canadensis* L.: seedlings thirty-five.

About 15 per cent of the area was covered by Acer-Tilia-Sambucus Associes.

The subdominants based on transect counts were as follows:

Fraxinus sp., eight seedlings;
Smilax Bona-nox L., eight seedlings;
Liriodendron tulipifera L., eight seedlings.

The subdominant herbs recorded in the quadrat but not in the transect were as follows:

Erythronium sp., 30.0 per cent,
Viola pubescens Ait., 20.3 per cent,
Dentaria laciniata Muhl., 14.5 per cent, and
Ribes sp., 13.5 per cent.

Invertebrates

Quantitative

Here, as elsewhere in this study, the invertebrates of one square meter of soil exceeded those of the 48 sweeps, and in most cases the excess was great. It was only in October that the specimens were greater in the sweeps than in the soil samples. Nothing was taken in the sweeps from December through April. The months in which specimens were collected in sweeps, in order of abundance, were as follows: October, September, July, June, May, August and November. These were the only months in which specimens were taken through sweeps.

Autumnal period (September 30 to November 30): From October 19 to the 31, the average number of invertebrates found in the soil per square meter was fifteen, in 48 sweeps fifty-nine. The temperature had already dropped but perhaps not sufficiently to cause the migration of the invertebrates back toward the surface nor to cause the insects to leave the herbs and shrubs and take cover at the surface or within the ground. The temperature was 56.12° in the soil, 61.52° at the surface and 71.42° in the air. The rainfall was 1.18 inches and the relative humidity 62 per cent.

The next period, the first half of November, the soil fauna remained unchanged, while a great decline in sweeps occurred. The temperature dropped considerably; but the rainfall decreased.

During the last half of November the fauna of both the soil and sweeps increased. The temperature had received a great slump and the rainfall and relative humidity were also less.

Hiemal period (November 30 to March 15): For the first half of December the soil fauna decreased and nothing was taken in the sweeps. The temperature was a little less than the preceding period. The rainfall and relative humidity were much higher.

From December through April nothing was taken in the sweeps, therefore, there will be no further reference to sweep specimens until May is discussed.

For the second half of December nothing was collected from the soil. Only one collection was made. The temperature of the soil was 37.40°, the surface 32° and the air 26.6°. The relative humidity was 88 per cent.

During the first half of January an average of 3.3 specimens per square meter of soil was collected. The temperature of the surface and air was about the same but the temperature of the soil was about 4° lower.

During the latter half of January nothing was found in the soil samples. The soil temperature was 33°, the surface 31.91° and the air 41.9°. The relative humidity was 58.5 per cent.

The first half of February had an average of five specimens per square meter of soil. The soil temperature was a little higher but the temperature of the air much lower. The relative humidity was 87 per cent.

For the last half of February the soil fauna contained five specimens per square meter of soil. The temperature of all three strata had increased. The relative humidity was 93.1 per cent and the rainfall 1.65 inches.

During the first half of March the invertebrates of the soil increased markedly over the preceding period, although the temperature and the relative humidity were a little less.

Prevernal period (March 15 to April 21): During the last half of March nothing was found in the soil samples. The temperature was somewhat higher and the relative humidity still high, 92 per cent.

For the first half of April the soil fauna averaged sixty per square meter of soil. The temperature was much higher, in the upper thirties and lower forties. The rainfall was 2.16 inches and the relative humidity 70.6 per cent.

Vernal period (April 21 to June 15): During the last half of April the soil fauna increased, and the temperature had also increased greatly. The rainfall was 1.60 inches and the relative humidity 54.4 per cent.

During the first half of May the number of soil invertebrates decreased, and for the first time since the last half of November specimens were taken in sweeps, only four, averaging 1.3 specimens per 48 sweeps. The temperature of the soil was about 3° higher, but the temperature of the surface and air was less than that of the preceding period.

The last half of May brought an increase in both soil samples and sweeps. The temperature was much higher, in the sixties and lower seventies. The relative humidity was less, 69.5 per cent; the rainfall was 2.69 inches.

From June 1 to the 15, the fauna of soil and sweeps decreased. The temperature was 68° in the soil and 76.55° in the air. The rainfall was 4.12 inches and the relative humidity 60 per cent.

Estival period (June 15 to August 30): For the last half of June the specimens in both strata remained the same. The temperature was much less for this period than for the first half of this month. The rainfall was a little heavier and the humidity greater.

During the first half of July there was a slump in soil specimens, whereas there was an increase in the sweeps. The temperature was higher, about the same as for the first half of June. The humidity was less and the rainfall much less.

For the last half of July the soil specimens decreased markedly. The sweep specimens remained almost the same. The temperature had increased well into the seventies. The humidity was higher but the rainfall less.

For the first half of August the soil invertebrates again increased, forty per square meter, but the sweep specimens were much reduced. The temperature of all three strata was a little less than for the preceding period. The relative humidity was a little higher but the rainfall less.

For the last half of August the invertebrates of the soil decreased, but in the sweeps they increased. The temperature was about 3° less than it was during the first half of the same month. Both the rainfall and humidity were higher.

Serotinal period (August 30 to September 30): During the first ten days of September the invertebrates of both the soil and the sweeps increased. The temperature was lower than during the last half of August. The humidity was higher but the rainfall less.

In this associes the invertebrate fauna of the soil was greater, numerically, during the warmer than during the colder months. During the colder period, from November 16 to April 15, the average number per square meter was 17.5. The temperature of the soil between these dates ranged from 32.54° to 41.58°. From April 15 to September 10, plus the period from October 19 to November 15, the warmer period, the average number per square meter was 39.2. The soil temperature ranged between these dates, the warmer period, from 47.75° to 70.75°.

It has already been stated that this associes is much lower and holds water longer periods of time than the other communities studied. The retention of moisture is a factor here influencing the invertebrates to remain closer to the surface during the drier months of the summer, and hence a greater number was found during the warmer than the colder period.

Out of twenty-two periods or cases discussed in all cases, except nine, any increase or decrease in soil temperature also brought an increase or decrease in soil fauna. In three cases where a change of temperature occurred the number of animals was unchanged. The months listed, in order of abundance, as per number of soil invertebrates were as folows: May, June, April, March, September, August, July, November, October, December, February and January.

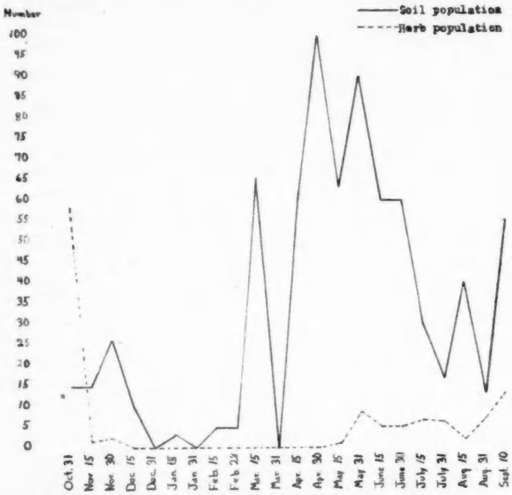

Fig. 9. Graphs showing the invertebrate population of the Herb and Soil strata of the Acer-Tilia-Sambucus Associes (Station IV). Counts based on number of specimens per square meter or per 48 sweeps. Graphs based upon collections covering approximately two-week periods.

Annotated List of Most Common Invertebrates

Oligochaeta

Diplocardia sp:—Sixteen specimens were collected. They were taken during the following months: November, December, April, May and June.

Lumbricus sp:—Thirty-four specimens were collected. They were taken during the following months: April, May, June, July and September.

Diplopoda

Polyzonium rosalbum Cope:—This species was collected in May, July and August.

Chilopoda

Geophillus strigosus McNeill:—This species was collected on January 11, in April, May, June and August. They were found in the soil samples. The soil temperature on January 11, was 35.06° and the surface temperature 33.8°.

Lithobius bilabiatus Wood:—This species was taken in the soil stratum during May, July and August.

Thysanura

Metajapyx sp:—These very primitive insects were taken in the adult stage during April, May and August.

Hemiptera

Lygus oblineatus Say:—This species was collected in the adult stage in October, November and June. They were limited to the sweeps.

Neides muticus Say:—Seven adults were collected in soil samples in July and September.

Homoptera

Philaenus leucophthalmus (L.):—This species was taken in the adult stage, in sweeps, in July, September and October.

Coleoptera

Paria canella Fab:—These beetles were collected in the adult stage, in sweeps, in May, June and October.

Ludius sp., *Melanotus* sp., and *Agriotes* sp:—Ludius specimens were collected during June and July. Melanotus were collected during April, May and August. Three specimens of Agriotes were taken in August. All three genera represented larvae and were collected from the soil.

Lepidoptera

Oleuthreutidae:—These larvae were collected in sweeps during October. They were fairly numerous.

Table 4. Predominants of the Acer-Tilia-Sambucus Associes (Station IV).

Species	Total Number	Number in Soil	Number in Sweeps	Average Number and Average Per Cent Per Meter Square or Per 48 Sweeps: Soil Number	Soil Per Cent	Sweeps Number	Sweeps Per Cent	Prevernal Period (March 15 to April 21)	Vernal Period (April 21 to June 15)	Estival Period (June 15 to August 30)	Serotinal Period (August 30 to September 30)	Autumnal Period (September 30 to November 30)	Hiemal Period (November 30 to March 15)
Lumbricus sp.	340	340	......	7.39	22.07	......	......	40	80	110	110	......	......
Diplocardia sp.	160	160	......	3.48	10.38	......	......	60	60	20	......	10	10
Geophilus strigosus McNeill	110	110	......	2.39	7.14	......	......	30	50	20	......	......	10
Oleuthreutidae	114	40	74	.87	2.60	1.61	29.6	......	20	......	......	94	......
Metajapyx sp.	80	80	......	1.74	5.19	......	......	......	60	20	......	......	......
Polyzonium rosalbum Cope	50	50	......	1.09	3.25	......	......	......	30	20	......	......	......
Lithobius bilabiatus Wood	41	40	1	.87	2.60	.02	.4	......	10	31	......	......	......
Paria canella Fab.	16	......	16	......	......	.35	6.4	......	2	1	......	13	......
Eupithecia sp.	10	......	10	......	......	.22	4	......	4	......	......	6	......
All other species	869	720	149	15.65	46.73	3.24	59.6	50	305	193	26	145	150
Totals	1790	1540	250	33.5	100	5.44	100	180	621	415	136	268	170

Eupithecia sp:—These insects were found in May, June and October, in the adult stage, in sweeps.

Phalaenidae:—These were taken in the larval stage during May, June, October and November. They were found in the soil and sweeps.

The number of species found among the invertebrate groups in the two strata were as follows:

	Soil	*Sweeps*	*Totals*
Coleoptera	6	13	19
Hemiptera	4	10	14
Araneida	3	6	9
Hymenoptera	3	4	7
Diplopoda	6	0	6
Chilopoda	1	5	6
Diptera	1	3	4
Homoptera	1	3	4
Isopoda	1	0	1
Neuroptera	0	1	1
Orthoptera	0	1	1
Lepidoptera	0	1	1
	26	47	73

FAGUS-ACER ASSOCIATION (STATION V)

This station was located in a climax Fagus-Acer Association. This association was adjacent to the Potentilla-Solidago-Rumex Associes. It was located nearest to human residence than any of the other communities. It was within seventy-five meters of houses. This community was bordered on the west, north and south by dirt roads. These roads ran along the edge of the woods. Much of the collecting was done within fifty meters of these roads. Another road ran directly through the collecting grounds of the station in a northeastern direction. This road after getting well within the woods continued but gave off a branch to the right and one to the left. Two other roads cut across this community in a southwest direction. All such roads were used mainly for getting wood but also for other purposes. Many of the smaller trees were still being cut and hauled away for fuel, etc. A layer of leaves about one inch deep covered the humus. The sod was about one inch thick; the humus about two inches deep. The herb coverage was about 30 per cent.

Vegetation

In the Fagus-Acer Association along a transect line of sixty-one meters the following dominants were recorded: *Acer rubrum* L., sixty-two under two inches in diameter and ten over two inches in diameter; *Fagus grandifolia* Ehrh., twenty-eight under two inches in diameter and eleven over two inches in diameter; as a matter of fact, out of these eleven trees three were between four and eight inches in diameter and eight were over eight inches in diameter. After entering this forest it could be observed that the dominants in many places were limited in number and stood some distance apart, especially the larger ones. But whether one was within the forest or some distance away, the large size and extreme height of the dominants over the other trees would give the observer no mistaken impression of what they were.

The subdominants based on quadrat counts were: *Claytonia virginia* L., 17.5 per cent and *Erythronium* sp., 58.6 per cent.
None of the plants, including the dominants, were well distributed.

Other plants recorded in the quadrat, in order of abundance, were: *Dicentra canadensis* (Goldie) Walp., *Fagus grandifolia* Ehrh., *Acer saccharum* Marsh., *Viola papilionacea* Pursh., *Panax quinquefolium* L. and *Euonymus obovatus* Nutt. Grasses were almost totally absent.

Invertebrates

Quantitative

The work at this station was commenced on October 30. The soil samples, as usual, yielded far in excess of the sweeps. Not a single case was found where the average number of invertebrates in 48 sweeps exceeded the average number in one square meter of soil. The months yielding specimens in sweeps, in order of abundance, were as follows: July, August, June, September, May, October and November. Nothing was taken in sweeps from December 1 to May 15.

Autumnal period (September 30 to November 30): The invertebrates for the last half of October were based on one collection which was made on October 30. The number of specimens found in one square meter of soil was 140 and the number in 48 sweeps three. The soil temperature was 49.64°, the surface 44.60° and the air 46°. The rainfall was 1.18 inches and the relative humidity 76 per cent.

For the first half of November the invertebrates of both strata decreased. In the soil the average number found in one square meter was seventy-five and in 48 sweeps 1.5. The temperature had dropped to about 45°. The relative humidity was 68 per cent and the rainfall .86 inches.

For the last half of November the fauna of both strata decreased appreciably. The temperature had dropped between 5° and 10°. The rainfall was less but the humidity much higher than for the preceding period.

Hiemal period (November 30 to March 15): For the first half of December the soil fauna again decreased, averaging twenty-five specimens per square meter. Nothing was taken in the sweeps. The temperature had received another drop, it stood as follows: soil 39.75°, surface 35.42° and air 29.57°. The relative humidity and rainfall had increased, the former was 92 per cent and the latter 1.07 inches.

From December 1 to May 15, nothing was found in the sweeps, therefore, no further mention will be made of this stratum until the appropriate time is reached in the discussion.

For the last half of December the soil averaged ten specimens per square meter. Only one collection was made during this period of time. The soil temperature was 32°, the temperature of the surface and air was lower.

For the first half of January the average number of invertebrates per square meter of soil was thirty. The temperature of the soil and surface increased about 2°, the air temperature had increased even more. All temperatures were above 32°.

The invertebrate fauna of the soil, for the last half of January, decreased to five specimens per square meter. All three temperature readings also decreased. The relative humidity had decreased to 64 per cent.

For the first half of February the soil fauna increased greatly, there were 73.3 specimens per square meter. The temperatures had also increased but the relative humidity and rainfall decreased.

During the last half of February the invertebrates decreased, there were forty specimens per square meter of soil. The soil temperature was 33.43°, almost as low as it was during the last half of January. The relative humidity and rainfall were much higher than during the first half of February.

For the first half of March nothing was found in the soil samples. The temperature of the soil and surface was slightly lower, but that of the air higher. The humidity was only a little less.

Prevernal period (March 15 to April 21): During the last half of March ten specimens were taken in the soil samples. The temperature of the soil and surface was a little less, but the temperature of the air higher. The relative humidity and rainfall had increased over the preceding period.

During the first half of April the soil fauna increased to twenty specimens per square meter. The soil temperature increased up to 40.10°. The humidity had decreased but the rainfall increased.

Vernal period (April 21 to June 15): The last half of April the soil specimens dropped to zero. The temperature made a very marked increase, it was 48° in the soil and 59.36° in the air.

From May 1 to the 15, the average number of soil fauna increased to fifty-five, with the soil temperature remaining about the same. The air temperature dropped about 10°, but the relative humidity increased to 84.7 per cent.

From May 16 to the 31, the soil fauna increased slightly. For the first time since the last half of November specimens were taken in sweeps. All temperatures increased greatly. The rainfall also increased but the relative humidity dropped to 69 per cent.

During the first half of June the soil specimens decreased to about one-half the number collected during the preceding period. The sweep fauna now averaged 5.5 specimens per 48 sweeps. This was almost twice the number collected during the preceding period. The temperatures stood as follows: soil 74.66°, surface 72.77° and air 70.78°. The rainfall was 4.12 inches and the relative humidity 77.5 per cent.

Estival period (June 15 to August 30): From June 16 to the 30, the invertebrates of the soil increased to thirty-five per square meter, but the sweeps decreased slightly. The temperatures dropped considerably.

For the first half of July the soil fauna decreased markedly, but the sweep specimens increased. All temperatures increased appreciably.

During the last half of July the invertebrates of the soil decreased while in the sweeps there was an increase. All temperature readings increased. The humidity and the rainfall were less.

From August 1 to the 15, the soil specimens indicated an increase, whereas the reverse was true of sweeps. The temperature in the soil was higher but less on the surface and in the air.

During the last half of August the specimens in both the soil and sweeps increased. All temperatures were less. The rainfall and humidity were greater than during the preceding half month.

Serotinal period (August 30 to September 30): For the first ten days of September nothing was found in the soil and the sweep specimens were much reduced. All temperatures decreased over the last half month. The humidity was greater but the rainfall less.

Out of twenty-two cases all, except seven, with each increase or decrease of soil temperature there was also an increase or decrease in soil fauna. The rule held in every case during the colder months, except one. The remaining six exceptions occurred during the summer. This indicates that temperature was the potent factor influencing the vertical migration of soil invertebrates during the colder weather.

During the colder months, from November 16 to April 15, when the temperature ranged from 32° to 41.54°, the average number of specimens collected per square meter of soil was 25.8. During the warmer period, from April 16 to September 10, plus the time from October 13 to November 15, when the soil temperature ranged from 45.14° to 74.65°, the average number of invertebrates collected per square meter was 39.3. The immense amount of shade here in the beech-maple association, is perhaps a factor in the retention of moisture during the summer and

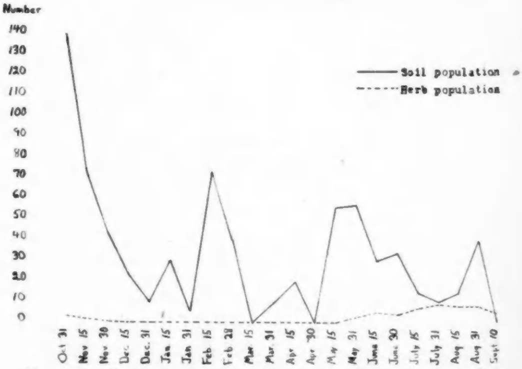

FIG. 10. Graphs showing the invertebrate population of the Herb and Soil strata of the Fagus-Acer Association (Station V). Counts based on number of specimens per square meter or per 48 sweeps. Graphs based upon collections covering approximately two-week periods.

hence a larger number of soil fauna was collected during the summer than during the winter. The months listed, in order of abundance, as per number of invertebrates were as follows: October, November, February, May, June, August, January, December, July, April and March.

Annotated List of Most Common Invertebrates

Oligochaeta

Diplocardia sp:—Only six of these earthworms were collected, some in May, November, February and March.

Helodrilus sp:—Four specimens were collected, one in May, one in June and two on February 21; the ground temperature on February 21, was 33.8°.

Lubricus sp:—Eight specimens were taken. They were collected on January 11, February 13 and in April. The ground temperature on January 11, was 35.96° and on February 13, it was 35.06°.

Chilopoda

Geophilus strigosus McNeill:—These centipedes were collected in the soil stratum in February, April, May, June, July and December.

Thysanura

Metajapax sp:—These insects were in the adult stage. They were collected during April, May, November and December. Comstock referred to these primitive insects as being uncommon.

Hemiptera

Nabis sordidus Reut:—Specimens were collected in July, August and September, mostly in the herb stratum.

Homoptera

Philaenus leucophthalmus (L.)—This species was limited in the collections to July and August. They were found in sweeps and in the adult stage.

Coleoptera

Agriotes sp. *Ludius* sp. *Melanotus* sp:—All three genera were wireworms and were taken in the soil stratum. Three specimens of Agriotes were collected on October 30. Ludius specimens were collected in October, November, on December 4, January 4 and February 13. On January 4, the soil temperature was 32.36° and on February 13, the temperature was 35.06°. Specimens of Melanotus were collected in June, July, August, September and November.

Anaedus brunneus Ziegl:—This species was collected at this station during October, November and May. They were in the adult stage and found in the soil.

Diptera

Bibio longipennis Lw:—This species of Diptera was taken in the adult stage from both soil samples and sweeps, but mostly from sweeps. They were collected in June, July, October and November.

The number of species found among the invertebrate groups in the two strata were as follows:

	Soil	*Sweeps*	*Totals*
Coleoptera	5	10	15
Diptera	5	4	9
Araneida	5	4	9
Hymenoptera	1	7	8
Hemiptera	3	2	5
Diplopoda	4	0	4
Chilopoda	3	0	3
Lepidoptera	0	3	3
Pulmonata	1	0	1
Isopoda	1	0	1
Homoptera	0	1	1
	28	31	59

The predominants in the Fagus-Acer Association appear to be markedly scarce both as species and as individuals.

TABLE 5. Predominants of the Fagus-Acer Association (Station V).

Species	Total Number	Number in Soil	Number in Sweeps	Average Number and Average Per Cent Per Meter Square or Per 48 Sweeps				Preverval Period (March 15 to April 21)	Vernal Period (April 21 to June 15)	Estival Period (June 15 to August 30)	Serotinal Period (August 30 to September 30)	Autumnal Period (September 30 to November 30)	Hiemal Period (November 30 to March 15)
				Soil		Sweeps							
				Number	Per Cent	Number	Per Cent						
Ludius sp.	130	130		3.02	9.02				20	10		40	60
Geophilus strigosus McNeill	110	110		2.56	7.63			10	60	10			30
Metajapyx sp.	90	90		2.09	6.25			10	20	20		30	10
Anaedus brunneus Ziegl.	81	80	1	1.86	5.55	.02	.87		10	1		70	
Lumbricus sp.	80	80		1.86	5.55			10					70
Melanotus sp.	70	70		1.63	4.86					60		10	
Helodrilus sp.	40	40		.93	2.78				10	10			20
Agriotes sp.	32	30	2	.70	2.08	.04	1.74		2			30	
Diplocardia sp.	70	70		1.63	4.86			10	10			40	10
Bibio longipennis Lw.	27	20	7	.46	1.39	.16	6.08		3	13		11	
Nabis sordidus Reut.	14	10	4	.23	.69	.09	3.48			13	1		
All other species	811	710	101	16.51	49.30	2.35	87.77	10	225	186	3	157	230
TOTALS	1555	1440	115	33.48	100.	2.66	100.	50	360	323	4	388	430

THE EFFECTS OF DISTURBANCE

The initial steps in disturbance might be summed up as follows:

1. Destruction of natural vegetation.
2. Destruction of native animal life, partially in consequence of the elimination or reduction of hiding, feeding and breeding places. This can be looked upon as the removal of "economic opportunity" for the native species.
3. Introduction of new species through the influence of man, directly or indirectly.
4. The increase of individuals of certain species which are able to adapt themselves to man-modified areas. This can be interpreted as the creation of "economic opportunity" for such species.

The end results of disturbance may be numerous and varied, some proving beneficial and some detrimental to man. In considering such secondary or disturbed communities as are discussed in this paper it must be remembered that man's assumption of the role of a dominant organism introduces two new aspects of control that no other organism shows. These are *degree* of dominance or disturbance and land use or *object* of the disturbance.

It is well known that an even relatively slight disturbance within a primitive community causes some of the larger mammals to disappear or become much reduced in numbers, although many of the smaller mammals and certain birds actually increase in man-modified areas. It is more difficult, however, to designate the effects of disturbance upon the invertebrates, as species of almost every group have been found wherever man dwells and within areas of very great disturbance. In fact, certain groups thrive and increase under conditions produced by man, for instance, certain cockroaches, bed-bugs, thysanurians, house-flies, etc. Also, most analyses of even primitive communities pay more attention to the larger vertebrates (those which are partially or completely reduced in secondary areas) while studies of the results of disturbance on invertebrates in primitive communities are not common. Moreover, practically all communities by this time have had some degree of disturbance. These factors make it difficult to find material with which to make comparison. However, some plant studies in such communities are available for comparison.

The effects of disturbance upon the community depends upon the nature, extent, and degree of the disturbance. In other words, the kind of disturbance and the length of time during which the community has been disturbed are important. Communities of the kind studied in this paper would not be disturbed as much as a cultivated field. Numerous species and individuals of plants and animals are herein recorded, whereas in a cultivated field the number of species would be comparatively small, although the number of individuals might be great. Whether or not disturbance has had a very marked influence in reducing the number of invertebrates, especially insects, depends largely upon the extent of the disturbance to the vegetation. Thinning of the vegetation brings about reduction in the number of invertebrates. The proximity of man, it appears, has little or no effect provided the vegetation has not been thinned out or reduced by cutting, fires, grazing, cultivation, or other means. The Potentilla-Solidago-Rumex Associes and the Solidago-Agrostis-Daucus Associes are the earliest stages in the developmental sere, being composed predominantly of herbs, but they stood highest in abundance of specimens. The Solidago-Agrostis-Daucus Associes stood highest in number of species and the Potentilla-Salidago-Rumes Associes stood third. On the whole in the forest communities where the herbs were thinnest the invertebrates were less numerous. The Fagus-Acer Climax Association with a very low herb coverage was poor in species and poorest in specimens. It therefore seems that the invertebrates are not very much reduced in number unless the vegetation among which they live has been reduced by disturbance in some way. Although it has been shown that earlier stages of most successions in undisturbed commuities have more species and individuals than later stages, for reasons other than the above, the writer believes that the above explanation is valid and not in conflict with any other concept.

In this study, as a whole, it appears that the number of invertebrate specimens is not large as compared to other studies. On the other hand, the number of species does not seem to be greatly reduced—varying between fifty-one and ninety-seven in the five communities studied.

The groups which seem most abundant in disturbed areas are Coleoptera, Hemiptera, spiders, centipedes, millipedes, ants and mosquitoes of the genus Aedes.

Since the introduction of new species is the result of disturbance, the author has tried to ascertain the names of such species. The United States Bureau of Entomology was able to designate only one insect on the list as being introduced and some authorities even consider it a circumpolar insect. The name follows:

Brachyrhinus sulcatus Fab.

The introduced Myriapoda are as follows:

Diploiulus luscus Meinert
Diploiulus londinensis Leach
Napoiulus minutus Brandt

Since the great majority of earthworms belonging to the family Lumbricidae was introduced from Europe, although no earthworms of this family were determined as to species in this work, there is no doubt that many introduced species of this family were included.

Studies of disturbed areas, however, have of necessity depended upon accumulation of a fairly thorough understanding of the structure and dynamics of primitive or undisturbed communities. Ecologists have frequently been rebuked for so diligently searching after the remnants of such fast disappearing areas. It is obvious that man must understand the effects

which he produces, intentionally or otherwise, upon the biotic balance if his control is to be intelligent. It is equally obvious that the study of primitive communities must come first.

SUCCESSION

Potentilla-Solidago-Rumex Associes: This associes had been completely disturbed because it was under cultivation about fifteen or twenty years ago. It was completely covered with grasses and forbs. It was also being invaded by seedlings of sumac, aspen, elm and wild cherry. The presence of such grasses as timothy, red top, panic, and wild oats was an indication of past cultivation and, perhaps, later grazing. The invasion by herbs and later by seedlings is an indication of a future shrub community. The following species of invertebrates were listed as predominants in this associes, but not as predominants in any other community: *Philaenus leucophthalmus, Dictyna volucripes* and *Galerucella cribrata.*

Solidago-Agrostis-Daucus Associes: The resemblance of this associes to the preceding one was noted through the similarity of grasses and forbs. This associes was obviously in a more advanced stage of development which was attested by much older, larger, and more numerous shrubs. It had been completely cut but not plowed. In addition to the similarity in vegetation of the two associes the following predominants were listed in both but not listed as predominants in any other community: *Phaleanidae, Coleophora* sp., *Graphops* sp., *Lygnus oblineatus, Cymus angustatus,* and *Phlegyas abbreviatus.* Such predominants being common to both communities, but not to any other, indicate something of a carry-over or a transition from the Potentilla-Solidago-Rumex Associes to the Solidago-Agrostis-Daucus Associes. But the difference between the two communities on the basis of predominants might also be pointed out. The following were listed as predominants in the Solidago-Agrostis-Daucus Associes, but not in any other community: Harpalus sp., Podabrus sp., Melanoplus sp., *Polydesmus moniliaris, Corythuca marmorata, Miridae, Euschistus euschistoides,* and *Photinus marginellus.*

The Quercus-Carya Associes and the Acer-Tilia-Sambucus Associes: The development of the Solidago-Agrostis-Daucus Associes might be in the direction of either one of the two above associes. On the basis of vegetation types, species composition and age, the Potentilla-Solidago-Rumex Associes and the Solidago-Agrostis-Daucus Associes seemed more related than the latter was to either the Quercus-Carya Associes or the Acer-Tilia-Sambucus Associes. In the latter associes the terrain was lowest of all communities and consequently much wetter. The Quercus-Carya Associes was on a higher elevation than any other community, hence the drainage was much better. The latter associes was located between the Solidago-Agrostis-Daucus Associes and the Acer-Tilia-Sambucus Associes and naturally its components entered into the two ecotones. Both associes had been subjected to partial cutting as well as other disturbance. The trees in the two associes were about the same height and diameter. Predominants listed and limited to the Quercus-Carya Associes were Sciara sp., Pardosa sp., *Dichomeris ligulella* and *Porcellio rathkei.* Those listed as predominants in the Acer-Tilia-Sambucus Associes but not so listed elsewhere were *Lithobius bilabiatus* and Eupithecia sp.

Fagus-Acer Association: This community had been less disturbed than any. There had been a slight amount of cutting. It was closer to human residence than any of the others. Its species composition, vegetation, etc., make it quite different from the last two communities discussed, yet both stand next to the Fagus-Acer in the developmental sere. The predominants herein listed, but not listed elsewhere were Agriotes, *Nabis sordidus,* and *Bibio longipennis.*

The data showed that in disturbed areas succession holds for invertebrates in both the soil and herb inhabiting forms.

SUMMARY AND CONCLUSIONS

This study comprised a man-modified area about 1.3 miles square. The approach was biotic. Five communities within the area were investigated.

The predominating soil is the Mahoning silty clay loam. The pH of the soil was acid, about five.

An analysis of the physical factors showed a marked decrease in the mean monthly air temperature from September 1939 through January 1940. The lowest mean monthly air temperature for the winter was 21.11° in January. Beginning with February the mean monthly air temperature increased each month until the highest was 73.52° in July. Beginning with August the mean monthly air temperature started its decline. Air temperature, during the winter, went much lower than temperatures on the surface or in the ground, frequently much below freezing. Surface temperatures rarely went below freezing; when they did the amount was very slight, not exceeding 1° or 2° below. Ground temperatures, as a rule, did not go much below freezing, but quite frequently approached the freezing point. The ground was much warmer in winter and much cooler in summer than the surface or air above. The surface is also warmer in winter and cooler in summer than the air above. This condition affords great protection to invertebrates which enter the ground during low temperatures in winter or high temperatures in summer. Invertebrates which are not adapted to burrowing into the soil will also find the surface, especially beneath vegetation and other objects, a warmer place in winter and a cooler place in summer than the air above.

In this study the total amount of rainfall in the Potentilla-Solidago-Rumex Associes, the field, from October 19, 1939 to September 10, 1940, was 29.35 inches. The total amount in the Fagus-Acer Association, the same period of time, was 31.83 inches.

The mean monthly relative humidity ranged from 64.72 to 86.4 per cent. The relative humidity of the winter months was somewhat higher than the summer months.

In all communities Coleoptera stood first in numbers of species. Hemiptera were second in all communities except the Fagus-Acer Association. In the latter community Diptera were second. This was the only community in which the number of dipterous species ran high. Araneida were third in all communities except the Quercus-Carya Associes. In this community Hymenoptera were third. Hymenoptera were fourth in all communities except the Quercus-Carya Associes. Here the Chilopoda were fourth. The Myriapoda were fifth in all communities except the Quercus-Carya Associes and the Fagus-Acer Association. In the Quercus-Carya Associes the Araneida were fifth and in the Fagus-Acer Association the Hemiptera fifth.

In every community the total number of specimens collected in one square meter of soil exceeded the total number in 48 sweeps. In most cases the excess was great. On the other hand, in every community except the Quercus-Carya Associes the total number of species collected in the sweeps exceeded those from the soil. But even in the Quercus-Carya Associes the number taken in the soil exceeded those from the sweeps by only one. The invertebrates from vegetation were much more numerous in species than those from the soil but those from the soil more numerous in specimens. The soil is a more uniform habitat than the vegetation. Uniformity of habitat makes for a limited number of species but the number of specimens might be great. Diversity of habitat makes for diversity of species but the number of specimens might be small.

Soil invertebrates were not equally distributed through the soil horizontally. The variation from counts in soil samples support this view.

Communities listed and their relative ranking in abundance of species and specimens were as follows:

	Species	*Specimens*
Solidago-Agrostis-Daucus Associes...	First	First
Acer-Tilia-Sambucus Associes.......	Second	Third
Potentilla-Solidago-Rumex Associes..	Third	Second
Fagus-Acer Association............	Fourth	Fifth
Quercus-Carya Associes............	Fifth	Fourth

In analyzing the number of soil invertebrates in relation to soil temperature, the period of study was divided into two general divisions, a cold and a warm period. The former period comprised the time with soil temperature ranging about 41° or 42° and lower, the latter period comprised the time covered by temperatures ranging about 45° and above. It was shown that in all communities, except the Acer-Tilia-Sambucus Associes and the Fagus-Acer Association, that the number of specimens from the soil samples during the colder period exceeded those during the warmer period. It was also pointed out that the retention of moisture, in these two communities, during the summer was perhaps responsible for the soil fauna being greater during the warmer than the colder period. Moisture is a more important factor in its influence on soil invertebrates during the summer than during the winter. During the summer if the ground dries out they will move down to follow the moisture; when it becomes moist again near the surface they will move back in that direction. Temperature seems to be the dominant factor in this connection during the winter. Temperature and moisture acting together during the summer may exert a very great influence upon the vertical migration of soil fauna. Many soil invertebrates are able to withstand freezing temperature and sometimes temperatures below freezing.

The total number of soil invertebrates in the five communities by month, listing each in order of abundance of specimens with the mean soil temperature will show the following data: November 43.09°, February 36.75°, May 53.20°, June 67.28°, March 32.66°, April 44.06°, January 33.53°, December 37.16°, August 62.55°, July 81.62°, to September 10, 62.55°. Work was discontinued on September 10. The months standing high on the list are those which are clearly within moderation in regard to temperature. Although some months low in soil population have temperatures within moderation but months running high are almost without exception those with moderate temperatures. In general no typical summer month with a high temperature stood very high in number of soil organisms, likewise no winter month with very low temperature stood very high.

In each community the predominants which have been named in tabular form show some repetition, but the data also show that the main components of each group of invertebrates in each community were different.

The invertebrate populations of both the herb and the herb-low-shrub stratum depended upon the seasonal presence and abundance of the predominantly annual vegetation.

On the basis of the foregoing facts the following conclusions can be drawn:

1. A series of successional stages due to disturbance of a deciduous forest area has been described.
2. Plant compositions of early stages of succession have been modified by disturbance.
3. The basic pattern of community succession has not been altered by disturbance.
4. The stage of succession at the present time depends on the amount and kind of disturbance and the length of time since disturbance has occurred.
5. The general phenomena of seasonal and ecological succession held for invertebrates in disturbed areas. This was true of soil as well as herb fauna. The same was also true of ecological succession in regard to plants.
6. Disturbance does not seem to bring about as significant a reduction in the invertebrates as in the vertebrates.
7. The proximity of man to the community may have little or no effect upon reducing the number

of invertebrates unless the amount of vegetation is reduced. Then the number of invertebrates is reduced.

8. During the winter, temperature is the most important physical factor affecting the vertical movement of the invertebrates of the soil.

9. Temperature and moisture acting together, during the summer, are the most important physical factors affecting the vertical movement of soil fauna.

10. Invertebrates within the soil are afforded great protection, during the winter, against outside low air temperatures. The same is true during the summer against outside high air temperatures.

11. The predominant organisms comprising the invertebrate groups of different communities are different.

12. On the average the number of species of invertebrates of the herb and shrub strata, taken through sweeps, was greater than the number of species of invertebrates of the soil stratum taken through soil samples. The reverse was true in regard to the number of individuals.

13. There is a significant difference between the number and kind of species found in the different communities. The same is true in regard to the number of individuals.

14. Coleoptera, Hemiptera and Araneida seem to be the most prevalent groups within the area studied. Dipterous insects were very scarce, except mosquitoes of the genus Aedes.

BIBLIOGRAPHY

Allee, W. C. 1911. Seasonal succession in old forest ponds. Trans. Ill. Acad. of Science. **4:** 126-131.

Beal, Geoffrey. 1935. Study of Arthropod population by the method of sweeping. Ecology **16:** 216-225.

Bird, Ralph D. 1927. A preliminary ecological survey of the district surrounding the Entomogical Station at Treesbank, Manitoba. Ecology **8:** 207-220.

1930. Biotic communities of the Aspen Parkland of Central Canada. Ecology **11:** 356-442.

Blake, I. H. 1926. Comparison of the communities of coniferous and deciduous forests. Ill. Biol. Mono. **10:** (4) 1-148.

1931. Further studies on deciduous forest communities. Ecology **12:** 508-527.

Blatchley, W. S. 1910. Coleoptera of Indiana. Indianapolis 1-1386.

1920. Orthoptera of N. E. America. Indianapolis 1-784.

1926. Heteroptera of E. N. America. Indianapolis 1-116.

Bodine, Joseph H. 1921. Factors influencing the water content and rate of metabolism of certain Orthoptera. J. Experimental Zoology **32:** 137-164.

Cameron, A. E. 1913. General survey of the insect fauna of the soil within a limited area near Manchester. J. Econ. Biol. **8:** 159-204.

1917. The relation of soil insects of climatic conditions. Agr. Gaz. **4:** 663.

Carpenter, J. R. 1935. Fluctuations in biotic communities: I. Prairie Forest Ectone of Central Illinois. Ecology **16:** 203-212.

1936. Quantitative community studies of land animals. Journal of Animal Ecology **5:** 231-245.

1938. An Ecological Glossary. Norman, Okla. 1-306.

Clements, F., & Victor E. Shelford. 1939. Bio-Ecology. New York 1-425.

Comstock, J. H. 1925. An introduction to Entomology. Ithaca. 1044 pp.

1940. The Spider Book. New York 1-708.

De Long, D. M. 1932. Some problems encountered in the estimation of insect population by the sweeping method. Ann. Ent. Soc. Amer. **25:** 13-17.

Dowdy, W. W. 1937. The hibernation of certain Arthropod fauna of the soil. Proc. Mo. Academy of Science **3:** 116-117.

Esten, M. M. 1932. A statistical study of a beech-maple association at Turkey Run State Park, Parke County Indiana. Butler Univ. Bot. Studies **2:** 183-201.

Fichter, Edson. 1939. An ecological study of Wyoming spruce-fir Arthropods with reference to stratification. Ecol. Monogr. **9:** 185.

Folsom, Justus. 1922. Entomology with special reference to its ecological aspects. Philadelphia 1-502.

Gleason, H. A. 1924. The structure of the beech-maple association in northern Michigan. Mich. Acad. Sci. Arts, Letters, and Paper **4:** 285-296.

Gray, H. E., & A. E. Treloar. 1933. On the enumeration of insects population by the method of net collection. Ecology **14:** 356-367.

Hanson, H. C., & C. T. Vorhies. 1938. Need for research on Grassland. Sci. Mo. **56:** 230-240.

Hesse, et al. 1937. Ecological animal geography. New York 1-597.

Holmquist, A. M. 1926. Studies in Arthropod hibernation. Ann. Ent. Soc. Amer. **19:** 395-426.

Illick, J. S., & Leroy Frantz. 1928. The beech-birch-maple forest type in Pennsylvania. Penna. Dept. Forest and Water Bull. **46:** 40.

Jacot, Arthur P. 1940. The fauna of the soil. Quarter. Rev. Biol. **15:** 28-58.

King, K. M. 1927. A quantitative investigation of the fauna of native and ruderal associations at Saskatoon, Saskatchewan with special reference to climate influence. Bulletin Ecol. Soc. Amer. **8(4):** 5.

Klugh, A. Brooker. 1923. A common system of classification in plant and animal Ecology. Ecology **4(4):** 366-377.

Mail, G. A. 1930. Winter soil temperatures and their relation to subterranean insect survival. Jour. Agri. Res. **41:** 571-592.

1935. Cold weather and its effects on injurious insects. Montana State College Agr. Expt. Sta. Circ. 146.

McAtee, W. R. 1907. Census of four square feet. Science **26:** 447-448.

McCollock, J. W., & W. P. Hayes. 1922. The reciprocal relations of soil and insects. Ecology **3:** 288-299.

1923. Soil temperature and its influence on white grub activities. Ecology **4:** 29-36.

Morris, H. M. 1920. Observation on the insect fauna of permanent pasture in Cheshire. Ann. Appl. Biol. **7:** 141-155.

Olson, Henry W. 1928. The earthworms of Ohio. Ohio Biol. Sur. Bull. **4:** (17): pp. 47-90.

Pettinger, N. A. 1935. A useful chart for teaching the relation of soil reaction to the availability of plant nutrients to crop. Bulletin of Virginia Agricultural and Mechanical College and Polytechnic Institute and the U. S. Dept. of Agr. 136.

Phillips, J. F. V. 1931. Quantitative methods in the study of numbers of terrestrial animals in biotic communities. Ecology **12:** 633-649.

Romell, L. G. 1932. Ecological problems of the humus layer in the forest. Cornell Univ. Agr. Exp. Sta. Memoir 170.

Sanders, N. J., & Victor E. Shelford. 1922. A quantitative and seasonal study of a pine dune animal community. Ecology **3**: 306-321.

Shackelford, M. W. 1929. Animal communities of an Illinois prairie. Ecology **10**: 126-154.

Shelford, Victor E. ——. Vegetation and the control of land animal communities. Biol. Bull. **23**: 59-99.

1912. Aspects of physiological classification. Biol. Bull. **23**: 331-370.

1926. Terms and concepts in animal Ecology. Ecology **7**: 3-69.

1931. Some concepts of Bio-Ecology. Ecology **12**: 445-467.

1937. Animal communities in temperate America. Chicago 1-324.

Smith, V. G. 1928. Animal communities of the deciduous forest succession. Ecology **9**: 479-500.

Taylor, W. P. 1927. Ecology or Bio-Ecology. Ecology **8**: 280-282.

U. S. Dept. of Agr., Weather Bur. 1938-1940. Monthly Meteorological summary Cleveland, Ohio.

Van Deventer, W. C. 1939. Studies on the Ecology of secondary communities in a deciduous forest area. Ecology **20**: 198.

Vestal, A. G. 1914. Internal relations of terrestrial associations. Amer. Nat. **48**: 413-445.

Walton, W. R. 1928. Earthworms as pest and otherwise. U. S. Dept. Agri. Farm. Bull. 1569.

Weaver, J. E., & F. Clements. 1929. Plants Ecology. New York 1-520.

Wellhouse, W. H. 1926. How insects live. New York 1-435.

Wesse, A. O. 1924. Animal Ecology of an Illinois elm-maple forest. Ill. Biol. Monogr. **7**: 1-93.

Williams, A. B. 1936. The composition and dynamics of a beech-maple climax community. Ecol. Monogr. **6**: 318-408.

Williams, Stephen R., & Robert A. Hefner. 1928. The millepedes and centipedes of Ohio. Ohio Bio. Surv. Bull. **4**: 18.

Wolcott, G. 1937. The animal census of two pastures and a meadow in northern New York. Ecol. Monogr. **7**: 1-90.

Yapp, R. H. 1922. The concept of habitat. Jour. Biol. **10**: 1-17.

MOUNTAIN CLIMATES OF THE WESTERN UNITED STATES

FREDERICK S. BAKER
Department of Forestry, University of California

TABLE OF CONTENTS

MOUNTAIN CLIMATES OF THE WESTERN UNITED STATES

The study of the climatic features of the United States is simplified by many excellent maps—notably those in the Atlas of American Agriculture and publications of the United States Weather Bureau—whenever regions of low relief are involved. For the western mountain ranges with steep slopes and great elevations, however, the maps are practically useless: they cannot well show the elevations at which the isoclimatic lines were drawn. Even with the addition of contour lines and the use of generous scales, maps are inadequate and unsatisfactory.

This paper aims to summarize the present published information on the climate of the western mountain ranges so that one may easily read the essential climatic data for specific elevations—particularly those features that are held to affect plant distribution.

To this end the mountainous portion of the western United States has been divided into twenty-eight areas numbered and located as shown on the map (Fig. 1). For some of these areas, especially along the immediate Pacific Coast, the main facts are adequately presented by conventional maps. The differences in elevations there are not great, and the climate is influenced more by distance from the sea than by elevation. In other regions—for example the Great Basin—there are too few data to reveal the trends of climatic change with elevation. For all the major mountain masses, however, graphs have been prepared to show:

1. The changes in temperature with elevation, January and July
    a. mean miximum
    b. mean minimum
    c. mean
    d. highest observed
    e. lowest observed

2. The changes in the length of the conventional "growing season" (the period during which the mean temperature exceeds 42°F.) and of the frostless season, as given by the U. S. Weather Bureau, with elevation.

3. The percentage of the annual precipitation that falls in each month—a figure little affected by elevation.

4. The total annual precipitation as it varies with elevation.

5. The total annual snowfall in its relation to elevation.

Table 1 in appendix A permits a fair computation of the monthly mean temperatures for months other than January and July, with some approximation of the mean maxima and minima for such months. Table 2, in appendix B, permits gauging the variation in rainfall for any given month; it shows the percentage of years in which the month will be rainless, will have less than half the normal (mean), and will have over double the normal. These graphs and tables have been prepared from published data of the Weather Bureau (Climatological Summaries of the United States by Sections). Often, because of the number and distribution of the stations, the graph lines have had to be drawn from very limited information. In order that there may be no illusions as to the reliability of the graphs, the charts show the individual points upon which the curves are based. These indicate effectively, though not concretely in a statistical sense, the adequacy of the supporting data.

CHARACTERISTICS OF MOUNTAIN CLIMATES

To prevent unwise use of these graphs and tables, certain characteristics of mountain climates, in regard to both temperatures and precipitation, should be noted.

Temperatures

That temperature decreases with increasing elevation is a well-known fact. The accepted value of the average lapse rate on mountains of the temperate zone is usually taken as 3.3 degrees F. per 1,000 feet rise, though of course there is considerable variation with season and between different regions. In the mountains of the western United States the rate averages 3.5 degrees F. per 1,000 feet in July, and 2.9 degrees in January. The annual average, though not computed, obviously lies close to the accepted figure of 3.3 degrees per 1,000 feet. In July the mean maximum temperatures have a more rapid lapse rate (4.0 degrees F. per 1,000 feet), and the mean minimum drops correspondingly slowly (2.9 degrees F. per 1,000 feet), so that the diurnal range decreases 1.1 degrees per 1,000 feet of rise. In January these differences are generally much less, and both the mean maximum and mean minimum fall about equally fast—2.9 degrees per 1,000 feet. Some charts show rather wide departures from these averages, especially in winter, as will be noted. The explanation lies, doubtless, in the small number of stations and the irregular distribution of those that show pronounced temperature inversions.

Temperature Inversions

At night, whenever there is no effective stirring and mixing of air layers by the winds, a well-defined local stratification of the air masses develops close to ground level. The cold air gathers in flat-bottomed valleys, flows down the steeper ravines, and leaves the intervening ridges relatively warm. These temperature inversions are much influenced by topographic form, being highly developed in broad, flat

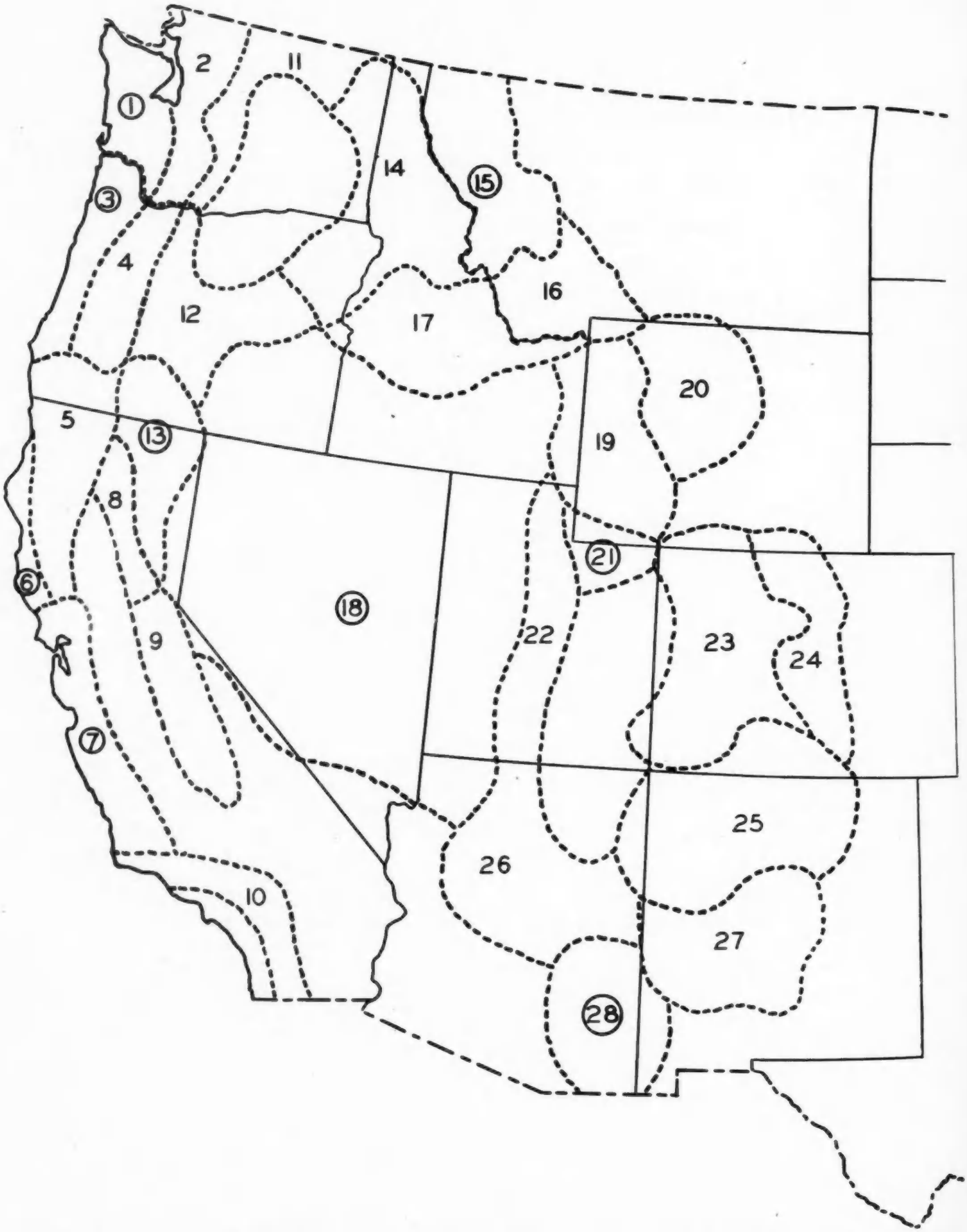

FIG. 1. Map of western United States showing areas of mountains included in this study. Areas are taken up in the order of numbering. No climatic charts are included for areas where the number is circled.

mountain valleys, from which air drainage is poor. They are also determined somewhat by natural windiness and by other minor factors. They are so pronounced as to mask any relation between "lowest observed temperatures" and elevation, as in Area 22 (Utah), Area 25 (Northern New Mexico), Area 14 (North Idaho), and elsewhere.

PRECIPITATION

Although rainfall naturally increases with elevation in the mountains, the rate of increase varies so much that no calculated average has any real value. In these mountains of the West, there is a zone of maximum rainfall at an elevation of a few thousand feet on the west slopes of the Cascade Range and the Sierra Nevada, well within the range of observer stations. Elsewhere the precipitation continues to increase to the crests of the mountains, or the elevation of maximum is at such high altitudes that no observations have been made. The correlation of precipitation and elevation is greatly modified, however, by three extraneous factors: approach effects, rain shadows, and what may be called canyon effects.

APPROACH EFFECTS

When a mountain range lies athwart the wind, the air masses are forced upward. The cooling effect so produced is basically the reason for the increase of rainfall with elevation. This effect first becomes noted, however, some distance to the windward of the mountains—the more so if they are steep, high, and massive. Thus the rainfall increases somewhat before the altitude begins to increase notably. This effect is particularly evident along the immediate Pacific Coast, where the stations are all essentially at sea level. Obviously the rainfall is much influenced by the type of topography lying immediately inland from the station. If the coast is steep and bold, the rainfall is relatively heavy; but if it is low and flat, the rainfall is less than the local average. The same effect can also be noted along the edges of the great valleys and plains near the mountains, as well as within the mountains themselves on the windward sides of bold high ridges.

RAIN SHADOWS

On their lee sides, mountains have a rain shadow, or zone where precipitation is much reduced as the rain-bearing winds are "milked dry" in their passage over the mountains. These shadows are often marked by strikingly low rainfall in certain localities and explain why many parts of Colorado, Wyoming, Oregon, and Nevada are dry despite their relatively high elevation. In these rain shadows, rainfall usually decreases with distance from the mountain crest to a certain region of minimum; and within this whole zone the altitudinal effects are obscured. The windward edge of the rain shadow may coincide with the crest of the mountain or may be part way down the lee side, thus further obscuring the altitudinal relations of the lee slopes.

CANYON EFFECTS

Rainfall recorded at stations in canyons and deep valleys may be far heavier than is characteristic of the elevation. Excluding approach effects, such rainfall is strongly influenced by the major surrounding ridges that have much higher altitude, for it is these that force the air masses to rise. Thus, even where such a great canyon as that of the Columbia River crosses the Cascade Range, the series of stations along the river are influenced by the mountain masses on either side. Though the elevations of the stations from Vancouver to Big Eddy vary less than 100 feet, yet the rainfall increases from 37 inches a year at Vancouver to a maximum of 78 inches at Cascade Locks—an amount characteristic of an elevation 2,500 feet in the mountains. Then, in the rain shadow, the precipitation diminishes to 12 inches at Big Eddy.

SOURCES OF ERROR

All these graphs and tables contain errors in a statistical sense. The errors may be large where the data are scanty or where there is great variation dissociated from the effect of elevation. At the same time less obvious, but probably large, systematic errors occur because most of the Weather Bureau cooperative stations are located on valley flats at inhabited towns, on farms, at railroad stations, or at dams and powerhouses—all in places where frequent temperature inversions produce abnormally low night temperature means and where the "canyon effect" causes relatively high precipitation as compared with "average" country at the given elevation. There is no way to allow for either of these factors with the data now available.

In short, the figures and graphs here presented are only preliminary and must be used with caution. They have been carefully compiled, however, and agree well with many climatic maps of the areas studied.

EXPLANATION OF THE CHARTS AND GRAPHS

For each area there are two sets of graphs—one dealing with the temperature climate, the other the rainfall climate. The first set consists of three charts. The upper chart gives the temperature-altitude relations for July. The left-hand graph line (data indicated by •) represents the lowest temperature of record. The next is the line for the mean minimum temperature (marked by +), followed by that of the mean temperature in the middle (marked O). The next to the right is the graph of the mean maximum temperature (marked X); and the last on the right is the highest recorded temperature (marked •).

Immediately below this is a similar chart showing the relations in the month of January.

The third chart at the foot of the page shows the growing season by four graph lines. The two solid lines pertain to the "growing season" used conven-

tionally by many ecologists, during which the mean temperature is above 42°F. The solid line that begins at or near the upper left edge and crosses the face of the chart, represents the length of the growing season in days, reading the lower set of figures along the bottom. The other solid line (or pair of lines) indicates the start of the "growing season" in spring and its close in the autumn. At a little lower level, two broken-line curves of similar form mark the length of the frostless season and the dates of the last spring and the first autumn frost. For convenience this chart assumes thirty-day months; further accuracy is unwarranted.

The second group of charts covers the precipitation climate of the area. The percent of rainfall in each month is indicated in the ordinary way; it changes but little with elevation. The precipitation-elevation and snowfall-elevation graphs that follow are conventional and require no comment.

The tables are explained in appendix A, which shows how to derive mean temperature for any month. Appendix B permits one to estimate the variability of the rainfall.

More detailed information can, of course, be found in the publications of the Weather Bureau, the most complete being the *Climatic Summary of the United States*, which gives detailed data on temperature, rainfall, and dates of frost. This publication provided the basis of the present study.[1]

The U. S. Department of Agriculture Yearbook for 1941, *Climate and Man*, contains condensed summaries, small but clear state maps, and descriptions of the climate by states. Altitudinal effects are seldom covered with any detail.

In the *Atlas of American Agriculture* are large-scale maps showing, as well as maps can, the elements of climate that are important to agriculture.

Other publications of importance in certain areas are cited as they occur.

AREA 1—COASTAL WASHINGTON

Location and Topography

Western Washington, between the ocean and the foot of the Cascade Mountains, is a region of hills and low mountains, except in the Olympic Peninsula, where the Olympic Mountains rise steeply to about 8,000 feet.

Climatic Characteristics

Over most of this area the climate is affected more by distance from the ocean than by elevation. Climatic maps therefore reveal the nature of the climatic variations adequately, except in the Olympic Mountains. In these mountains there are only a few observation stations, all at relatively low elevations on the edges of the mountain mass; and it is therefore impossible to do more than assume crude analogies to the climate of the Cascade Mountains to the east (Area 2). The Olympic Mountains have a timberline 500 to 1,000 feet lower than that of the Cascades; evidently their climate is somewhat cooler. They cast a strong rain shadow to the northeast, extending almost across Puget Sound, as the maps clearly reveal; but the nature of the rain shadow on their own lee slopes is not clear.

AREA 2—WESTERN SLOPES OF THE CASCADE MOUNTAINS IN WASHINGTON

Location and Topography

The Cascade Mountains in Washington are a broad and physiographically complex range. At the Canadian border the distance from their western base to their crest is some 75 miles; and although the range is narrower farther south it remains a very extensive body of mountains. Geologically it represents a complex uplift of an old peneplain forming a great platform 4,000 to 8,000 feet in elevation, which has been greatly eroded, and upon whose western edge stand several extinct volcanoes. As a result, low altitudes are found far into the mountains in the deep valleys of such streams as the Skagit, Skykomish, Nisqually, and Cowlitz. On the other hand, high mountains rise abruptly from the western rim; and many elevations exceeding 10,000 feet are found west of the main divide, which is rarely more than 8,000 feet.

Climatic Characteristics

The climate is marked by unusually small temperature ranges both in summer and in winter—reflecting, in part at least, the large number of cloudy and rainy days. Though the general lapse rates of temperature with elevation are not far from average, at low elevations there are striking temperature inversions in summer. In this season the climate near sea level is distinctly cooler than at about 1,000 feet elevation, where the warmest temperatures are noted. The cause is the proximity of Puget Sound in the north and, in the south, the relatively free inflow of oceanic air.

Rainfall is heavy and the rate of increase is rapid up to a certain elevation, which, on the basis of scanty evidence, appears to be about 3,000 feet. Beyond this point the rainfall probably decreases slowly. Snowfall is heavy and retards the onset of spring, which is rapid in the northern tier of states. Most of the observation stations are in stream valleys; and the recorded rainfall is often poorly correlated with the nominal elevation of the station, because of "canyon effects."

The topography of these mountains hinders the correlation of climate and elevation, especially in view of the small number of well-placed stations

[1] The *Climatic Summary of the United States* is issued in sections, each of which contains a descriptive introduction pointing out many important characteristics of the climate. The following sections are useful in the mountainous regions of the West: Western Washington, Eastern Washington, Western Oregon, Eastern Oregon, Northeastern California, Northwestern California, Central California, Southern California and Owens Valley, North Idaho, South Idaho, Western Montana, Southwestern Montana, Western Wyoming, Northwestern Wyoming, Eastern Utah, Western Utah, Western Colorado, Northeastern Colorado, Southeastern Colorado, Northwestern New Mexico, Northeastern New Mexico, Southern New Mexico, Northern Arizona, and Southern Arizona.

(Fisher, 1934); the graphs must therefore be used with caution. As Piper and Beattie (1915) have noted, the timberline in this region is extremely variable. On Mount Rainier it is often 2,000 feet higher on the ridges than in the valleys. In general it is 6,000 to 7,000 or even 7,500 feet elevation.[2]

AREA 3—COASTAL OREGON

Location and Topography

Between the Pacific Ocean and the foot of the Cascade Mountains in Oregon are the broad Willamette Valley and a series of low forested mountain ridges parallel to the coast. South of the Rogue River the pattern is broken by the higher and more massive uplift of the Siskiyou Mountains, which on their easterly side pinch off the extension of the Willamette Valley southward and in southern Oregon meet the westerly spurs of the Cascade mountains at elevations of about 2,000 feet. The boundary between this area and Area 5 to the south cannot be accurately drawn, owing to the lack of climatological stations in southwestern Oregon, but may be taken conveniently as the Rogue River from Grants Pass to the ocean.

Climatic Characteristics

Since most of the climatological stations lie either along the immediate seacoast or in the Willamette Valley, the altitudinal trends cannot be ascertained. They are undoubtedly complex. Probably, since the mountains are generally low, the climatic elements vary more with distance from the sea than with elevation. Under such circumstances the available maps

[2] A number of papers have dealt with certain climatic features of this region. Piper and Beattie (1915) discuss the climate from the botanist's point of view in considerable detail. Henry (1919) in studying the increase of precipitation with altitude draws one example from this area. Several foresters, concerned with the relations among precipitation, humidity, lightning storms, and the incidence of forest fires, have analyzed these climatic factors. Munger (1925) gives graphs for many individual stations, showing the probability of effective rainfalls (from a forest-fire viewpoint) by 10-day periods through the summer. Shepard (1939) maps the distribution of mean drouth periods, maximum drouth periods, precipitation, and the frequencies of low humidity Morris (1934) discusses the incidence of lightning storms and includes maps showing their movement.

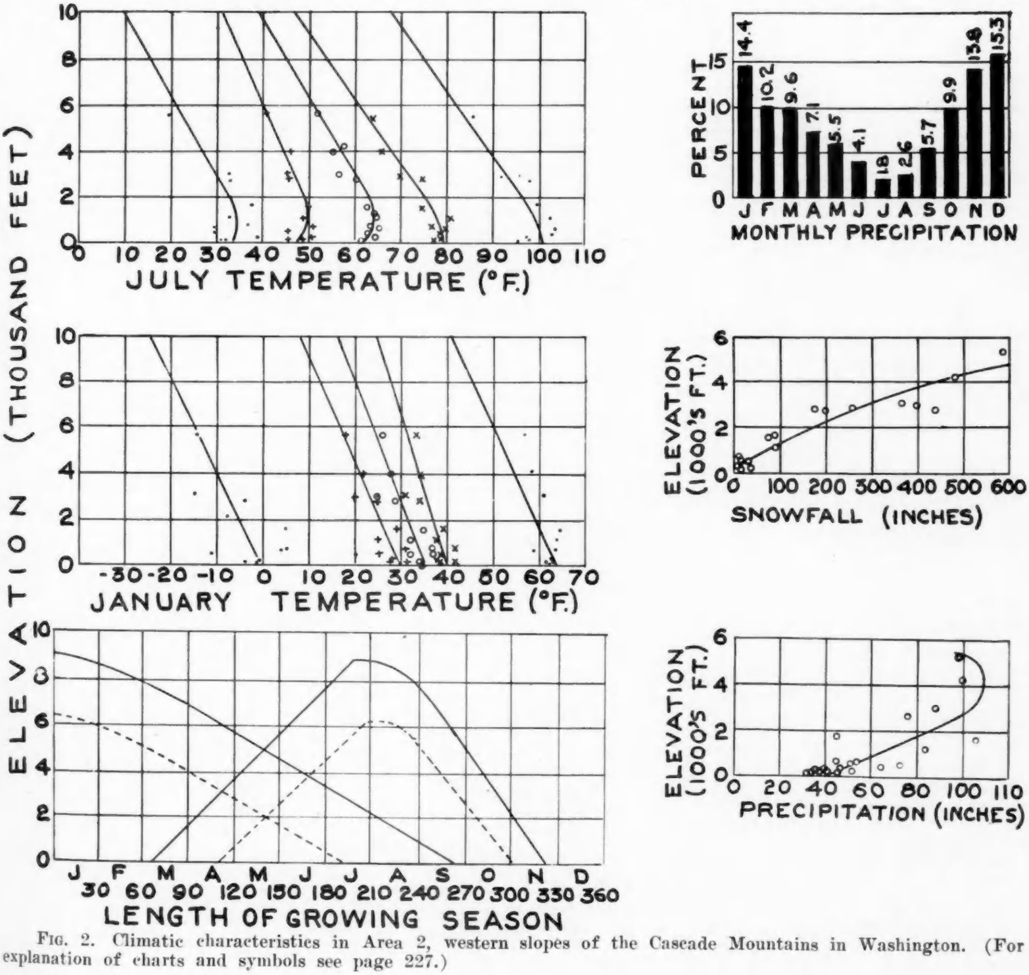

FIG. 2. Climatic characteristics in Area 2, western slopes of the Cascade Mountains in Washington. (For explanation of charts and symbols see page 227.)

are satisfactory. According to them, the climate becomes somewhat warmer inland, and rainfall amounts are greatly influenced by "approach effects" along the seacoast. At Glenora in the northern part of these coastal mountains the mean annual rainfall is 128 inches a year, the highest at any station in the United States having a long record.[3]

AREA 4—WESTERN SLOPES OF THE CASCADE MOUNTAINS IN OREGON

Location and Topography

The Cascade Mountains in Oregon, although not so broad a mountain mass there as in Washington, have developed the same type of elevated platform, into which such rivers as the Santiam, MacKenzie, and Willamette have eroded deep valleys, running back far into the high mountains. The extinct volcanic cones characteristic of the whole Cascade Range are located on or close to the main mountain crest, and the range is therefore simpler in a physiographic sense than the mountains in Washington.

[3] The work of Munger (1925), Morris (1934), and Shepard (1939) on fire weather is valuable in studying the mountain climate in this area. For details of their work, see footnote 2.

Climatic Characteristics

The lower slopes of the Oregonian Cascades drop down to the Willamette Valley for the most part and are cut off from the sea by the low Coast Range. They are therefore warmer than similar locations in Washington, quite aside from the fact that they are farther south. The lapse rate of the temperatures in summer appears unusually low here (2.3 degrees per 1,000 feet), whereas the diurnal range is unusually wide (32 degrees) and changes little with elevation. These peculiarities may, however, be only

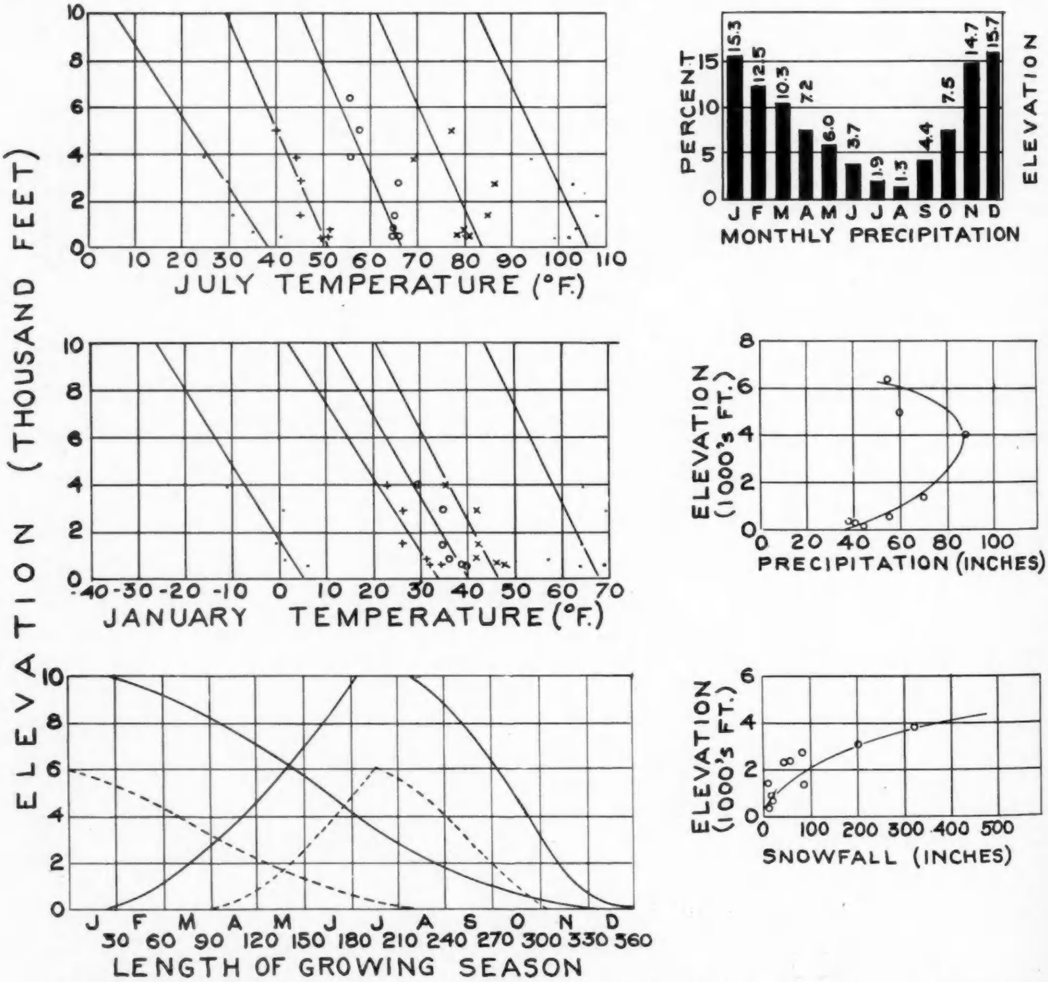

Fig. 3. Climatic characteristics in Area 4, western slopes of the Cascade Mountains in Oregon. (For explanation of charts and symbols see page 227.)

apparent, arising from insufficiency of data, for their cause is not obvious.

One feature of the rainfall climate is not shown by these graphs—namely, the deep rain shadow extending from the east side of the Klamath Mountains to the Cascade Range. Its full extent in the mountains cannot be mapped at present, since there are no stations in the critical area. In the valleys, however, and on the lower slopes the rainfall is unusually scant—only 20 inches a year, for example, in the vicinity of Ashland at an elevation of 2,000 feet, where the graph indicates 75 inches. In this relatively dry portion of the Cascade area the climate has many of the characteristics of Area 13, which lies to the eastward.[4]

AREA 5—KLAMATH MOUNTAINS AND INNER COAST RANGES OF NORTHERN CALIFORNIA

LOCATION AND TOPOGRAPHY

This area includes southwestern Oregon, south of the Rogue River and west of the Southern Pacific Railroad, which goes southward from Grants Pass; together with the associated mountains of northern California, south to the vicinity of Mount St. Helena. The area is marked by ill-defined ranges going under many names (the Siskiyou Mountains, Scott Mountains, Trinity Mountains) and having diverse geologic histories and physiographic forms. There is no well-developed pattern of crests and ridges, especially toward the north. Southward the general pattern of the whole Coast Range, that of ridges with a roughly north-south trend, develops. The area, in a physiographic sense, extends with only minor breaks to southern California; but in this study it is arbitrarily terminated at Mount St. Helena, beyond which the altitudinal trends are impossible to detect and climatic maps become the best recourse. The highest mountains are toward the north, where extensive masses reach heights of 6,000 to 8,000 feet. Between them are broad valleys and deep canyons. There are almost no true high altitude stations for climatic observations.

CLIMATIC CHARACTERISTICS

The climate here requires, for its full understanding, a study of both maps and profile graphs; it varies both with distance from the sea and with elevation. The region is very thinly populated, and the available climatological data can furnish only a bare framework for presenting climatic elements. In fact the north slopes of the mountains in southern Oregon constitute a large area within which there are no climatological stations at all. The graphs here presented apply only to those inland portions that do not receive the immediate effects of the ocean, particularly the summer fogs. At low elevations, nevertheless, some temperature inversion is noted in summer, due to the inflow of cool air from the sea. The temperature lapse rates have been based largely upon analogies between this region and the northern Sierra Nevada (Area 8). For July, however, the graph has been somewhat modified in accordance with Clark's observation that these mountains appear relatively warm and that plant associations extend about 1,000 feet higher than in the Sierra (Clark, 1937).

The mean annual precipitation varies greatly in different parts of the area, ranging from over 100 inches on the seaward slope of the Siskiyou Mountains to less than 20 in the rain shadow at their eastern base. Altitudinal relations are obscured because the rainfall decreases from the seaward slopes inland and from north to south. To attempt some generalized view of the situation, the data have been subdivided in the precipitation graph. Line A represents a region where elevation is practically unrelated to rainfall. This is the eastern third of the area lying from the head of the Applegate River in Oregon and thence southward along the east side of the line of high crests of the Siskiyou, Salmon, and Yolla Bolly Mountains and associated ranges that bound the Russian River drainage on its eastern edge, terminating in Mount St. Helena. Graph line C represents the rainfall in a region where the increase with elevation is very rapid. This area includes (in all probability) the drainage of the Illinois River in Oregon; the Smith River and west slopes of the Siskiyou Mountains; the Klamath River up to the junction of the Salmon; Trinity River to Hayfork; and the drainage of the Van Duzen, the Mad and most of the Eel and Russian Rivers to Mount St. Helena. These are mainly windward slopes with no great barrier ridges between them and the sea. The intermediate sector, represented by graph line B, lies essentially westward of the highest crests of the mountains, but is shielded on the west by ridges of considerable height. South of the head of the Eel River this zone becomes very narrow—almost nonexistent.

AREA 6—OUTER NORTHERN COAST RANGES OF CALIFORNIA

LOCATION AND PHYSIOGRAPHY

This area covers the seaward slopes and the country of relatively low ridges and mountains lying west of the Eel and Russian Rivers. It constitutes essentially the "redwood belt" or "fog belt" of this part of the coast and is profoundly affected in summer by the cold ocean waters to the west. It consists mainly of the drainages of many short rivers rising at elevations of about 3,000 feet and flowing westward to the ocean.

[4] There are a number of other valuable climatic studies covering this area. Wells (1922) considers the annual variability of rainfall here and elsewhere in Oregon. Dague (1929) has surveyed the records of low humidity in Oregon and presents numerous tables; relatively few mountain stations were, however, included. The studies of fire weather by Munger (1915), Morris (1934), and Shepard (1939), more particularly described in footnote 2, are also important in this area. Henry (1919) has mentioned the increase in rainfall between Portland and Mt. Hood. The climate in the Klamath rain shadow (including an isohyetal map) has been well discussed by Merriam (1936).

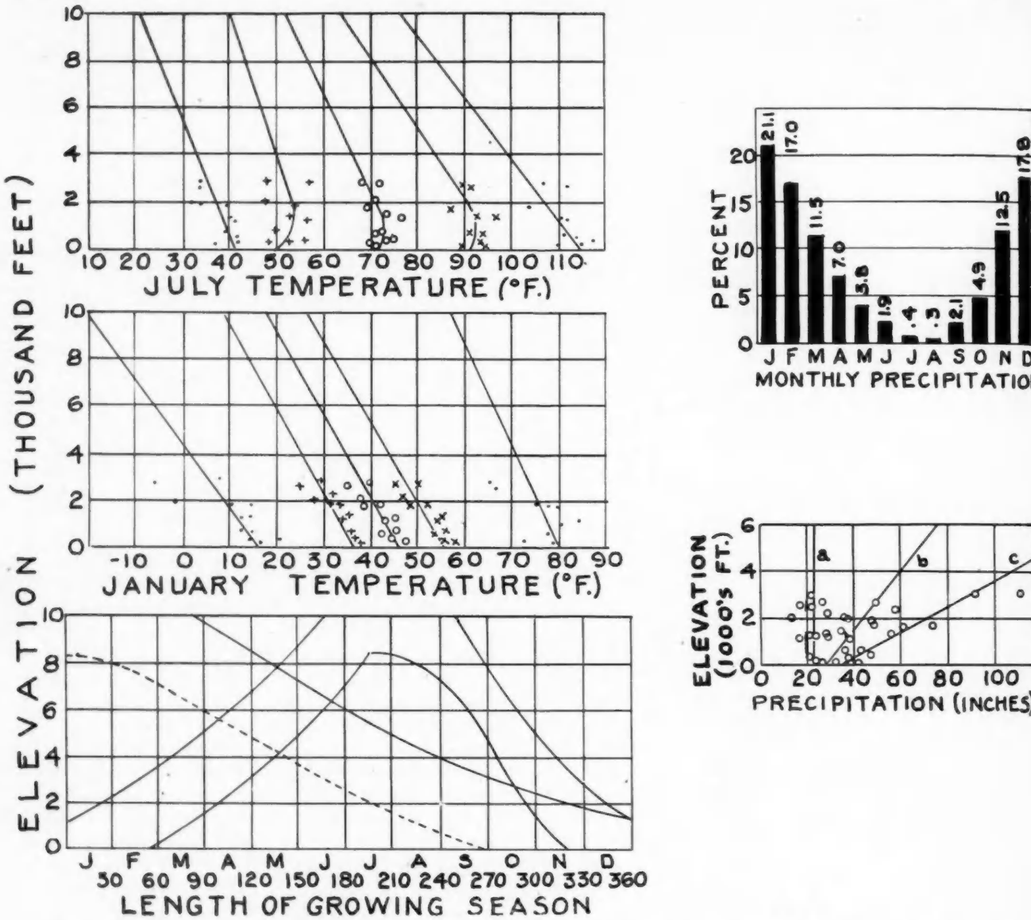

Fig. 4. Climatic characteristics in Area 5, Klamath Mountains and inner Coast Ranges of northern California. (For explanation of charts and symbols see page 227.)

Climatic Characteristics

As in Areas 1 and 3, the climate here changes sharply with distance from the ocean. As the sea water is colder off this coast than either to the north or to the south, its influence is intensified, and summer fogs are common and persistent. There are few climatic stations in this thinly populated region of dense forest of redwood and Douglas-fir, so that altitudinal trends cannot be determined. The changes that are correlated with distance from the sea can be read from climatic maps.

AREA 7—COAST RANGES OF CENTRAL CALIFORNIA

Location and Topography

This area includes all the coastal mountains from the Russian River and Mount St. Helena southward to the cross ranges of southern California and from the sea on the west to the Great Valley on the east. It is marked by several roughly parallel ranges running approximately north and south, separated, for the most part, by broad flat-bottomed valleys. The mountains are generally of no great height (3,000 to 4,000 feet) and, furthermore, are mostly broken by intervals of low hills or broad gaps that greatly affect the climate. These mountains bear scanty forest. Large areas are covered by an open oak woodland or brushy chaparral types.

Climatic Characteristics

The influence of the ocean is strongly felt, warming the area somewhat in the winter and rendering it very much cooler at low elevations in summer. At the latter season, the air in the interior valleys becomes intensely heated and rises. Cool oceanic air, therefore, blows in violently through major breaks and passes of the Coast Range and floods up the lateral valleys persistently if not always strongly. This mass of cool air varies in depth, but is usually

not much more than 3,000 feet deep; near the coast its upper limit is generally marked by a blanket of "high fog." The result is a complex mountain climate. The lower slopes are cool in proportion to their nearness to the ocean and the arrangement of valley patterns through which the oceanic air passes to the interior. In addition, mean temperatures usually increase somewhat with elevation, especially in the zone where the cold oceanic air is in contact with overlying warmer masses. As there are few stations in these mountains, one cannot well estimate the net effects of all these tendencies. Mount Tamalpais (2,375 feet elevation, 6 miles from the ocean) and Mount Hamilton (4,209 feet elevation, about 60 miles from the sea) indicate that at these elevations the summer temperatures do not differ greatly from those at about 4,000 feet in the Sierra Nevada. In January these mountains are considerably warmer, resembling Sierra Nevada elevations of about 2,000 feet.

The rainfall climate in the Coast Range is also complex, and that of the mountains seems poorly represented on published maps. On the immediate coast, approach effects are strongly marked, and the first slopes facing the ocean are well watered. The heavy rainfall apparently extends well over on to the lee slopes of such mountains as the Santa Cruz Range. In the valleys to the east, however, a rain shadow usually appears; and from there eastward are approach effects, altitude effects, and rain shadows, accompanying the whole series of ridges and valleys to the great valley of central California. In the absence of climatological stations neither maps nor profile graphs can present the complex situation. That the rainfall decreases greatly inland from the coast to the edge of the interior valley is well established and is evident from maps; but the intricate way in which it must decrease across the series of ridges and valleys is never shown effectively.[5]

AREA 8—WESTERN SLOPES OF NORTHERN SIERRA NEVADA

Location and Topography

This climatic area does not entirely coincide with the physiographic area represented by the title. On the north, beyond the North Fork of the Feather River, it covers mountains that belong technically to the Cascade Range, as far as Mount Shasta. The eastern edge of the climatic area is generally west of the water parting of the mountains; it follows a "climatic crest," which is marked by a line cutting across the drainage of the Pit and Feather Rivers, and connecting Mount Shasta, Mount Lassen, Spanish Peak, Pilot Peak, the Sierra Buttes thence to the topographic divide at the head of the Yuba drainage. Southward the climatic and physiographic crests coincide to Donner Pass, the southern limit of the area. The whole mountain mass is essentially a great tilted block deeply cut by canyons. Except for the volcanic peaks of Mount Shasta and Mount Lassen, the elevations rarely exceed 8,000 feet, and the mountains are forested from their crests down to the Digger pine-oak woodland that fringes the grassy Sacramento Valley.

Climatic Characteristics

Low elevations at the upper end of the Sacramento Valley are marked by very high temperatures, especially in summer. As a result, the temperature falls exceptionally fast with increasing elevation in the mountains. At the extreme north end of the region (the head of the Sacramento Valley), the relations of precipitation and elevation are much obscured by strong approach effects and perhaps canyon effects; the winds approaching the funnel-shaped end of the valley cause such unusually high rainfall that Redding, at 600 feet elevation, has some 37 inches. The amount increases sharply with elevation until the platform upon which lies Mount Shasta is reached. There in the rain shadow of the Klamath Mountains the effects are soon annulled, so that at 3,000 feet altitude the rainfall is under 30 inches. This situation is clearly shown by maps; but elsewhere the relation between elevation and rainfall is well indicated by the graphs here although precipitation decreases somewhat from the north to the south in this area. There are numerous stations, well distributed; and the graphs have a better statistical base than those of most areas.[6]

AREA 9—WESTERN SLOPES OF SOUTHERN SIERRA NEVADA

Location and Topography

From the point where the Southern Pacific Railroad crosses the Sierra Nevada, south to the Kern River canyon, this mountain mass represents a fairly uniform picture of a tilted block cut by deep canyons. Crest elevations increase generally southward to Mount Whitney and then drop rather quickly to the Kern Pass.

[5] Additional information regarding the summer temperature inversions in this area, as shown in the north end of the Santa Lucia Mountains near Carmel, is presented by Shreve (1927), who maintained a string of temperature stations running from sea level up as high as 5,000 feet elevation. The records, though short, broken and seasonal, show the temperature inversions very clearly. Cook (1934), who has studied the stream of cold air through the Sacramento River gap in the Coast Range, presents maps to show how it floods up the lateral valleys. Varney (1925) has thoroughly studied the variability of the rainfall from year to year; despite great variations in total amount, the degree of variation from the mean is fairly uniform throughout this area.

[6] Since the water supplies of the Sierra Nevada are exceptionally important to the valley communities of California, several studies have been made of the precipitation characteristics in these mountains. The increase of rainfall along the Southern Pacific Railroad east from Sacramento has been repeatedly discussed, one of the best studies being that of Henry (1919). A more extensive study of the rainfall pattern is that of McAdie (1914), who places the elevation of maximum rainfall at 5,000 feet and gives the rate of increase up to that point as 9.15 inches per 1,000 feet. More recently Varney (1920) has studied the rate of increase separately for each month. Sprague (1934) has shown that the snowfall in the Sierra Nevada varies less from year to year than the precipitation in the form of rain. His figures indicate an average snowfall of about 50 inches at 2,000 feet and 150 inches at 6,000 feet, the latter amount being considerably less than that shown in the graphs of this publication. Gray (1934) shows the existence of long-period fluctuations in precipitation in this area without attempting to determine the length of the cycles or their cause.

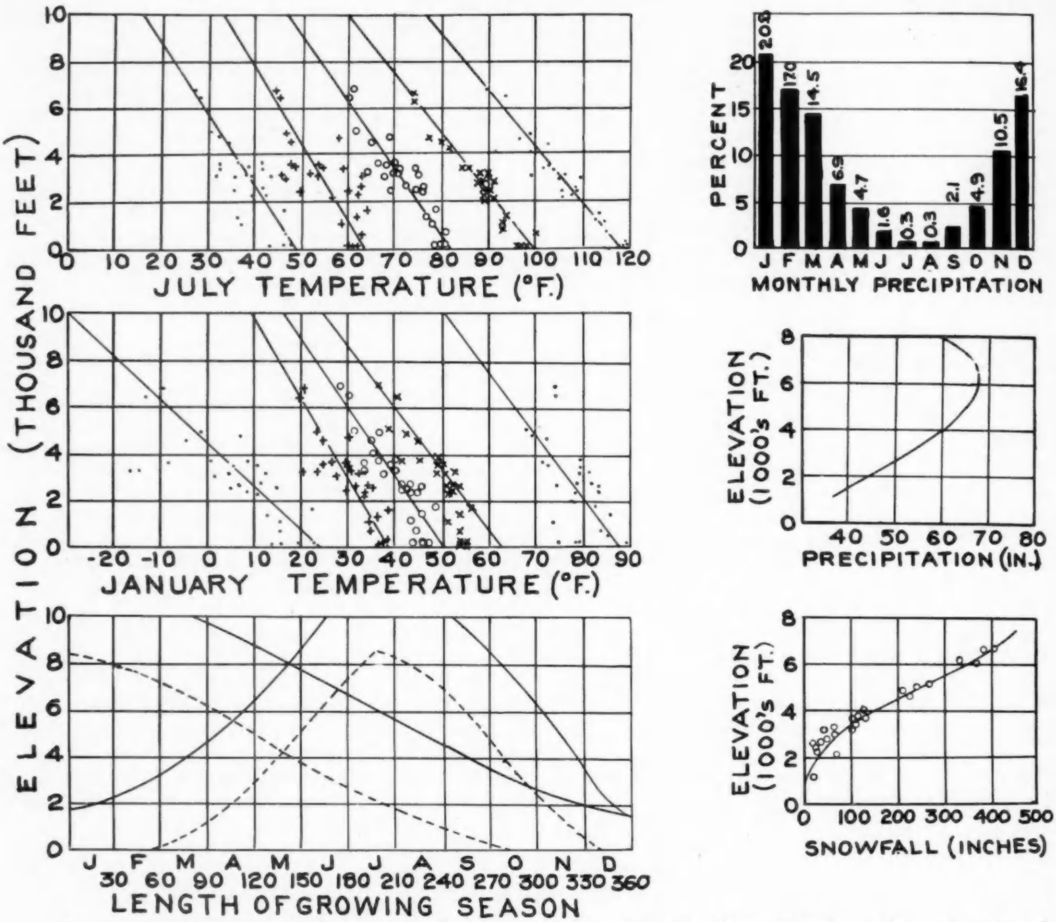

FIG. 5. Climatic characteristics in Area 8, western slopes of northern Sierra Nevada. (For explanation of charts and symbols see page 227.)

CLIMATIC CHARACTERISTICS

The mountains here are somewhat warmer than the northern section of the Sierra (Area 8); but the temperatures at the foot of the slopes in the San Joaquin Valley are not much warmer than farther north, especially in summer. As a result there is a less striking rate of cooling with increasing elevation here. The rainfall is less than farther north and decreases somewhat within this area, especially south of the Kaweah River. The precipitation is greatest at about 5,000 feet elevation. As there are many well-distributed stations in this region, the graphs are relatively dependable.[7]

[7] Besides the papers listed in footnote 6, which apply also to this area, a careful study of the precipitation increase with altitude has been made by Lee (1911), covering four sections across the mountain range between the Southern Pacific Railroad and the Yosemite region. He finds that the rate of increase from the valley to the zone of maximum averages about 8.5 inches per 1,000 feet. The rate shown in the present publication is nearer 10 inches. Little (1931) has also studied the broad climatic effects of the Sierra Nevada, showing that the range "piles up" the air on its western flanks, producing an abnormally high barometric pressure in the San Joaquin Valley and very high wind velocities across the crests.

AREA 10—SOUTHERN CALIFORNIA

LOCATION AND TOPOGRAPHY

The area comprised in this unit consists of several mountain masses going under a number of names and extending from near Santa Barbara eastward to the Cajon Pass and thence southward to the border of Lower California. These uplifts, of diverse geological history and topographic form, are marked by deep breaks and passes between them and by several high and rather isolated peaks—for example, Mt. San Jacinto. The desert-facing slopes are no doubt poorly reflected in the graphs. The Tehachipi Mountains from the "Ridge Route" around to Kern Pass are not included here (nor in any other area), for their climate is hardly computable from existing data.

CLIMATIC CHARACTERISTICS

In the western part of Area 9 the ocean lies at the foot of the mountains; but near San Bernardino

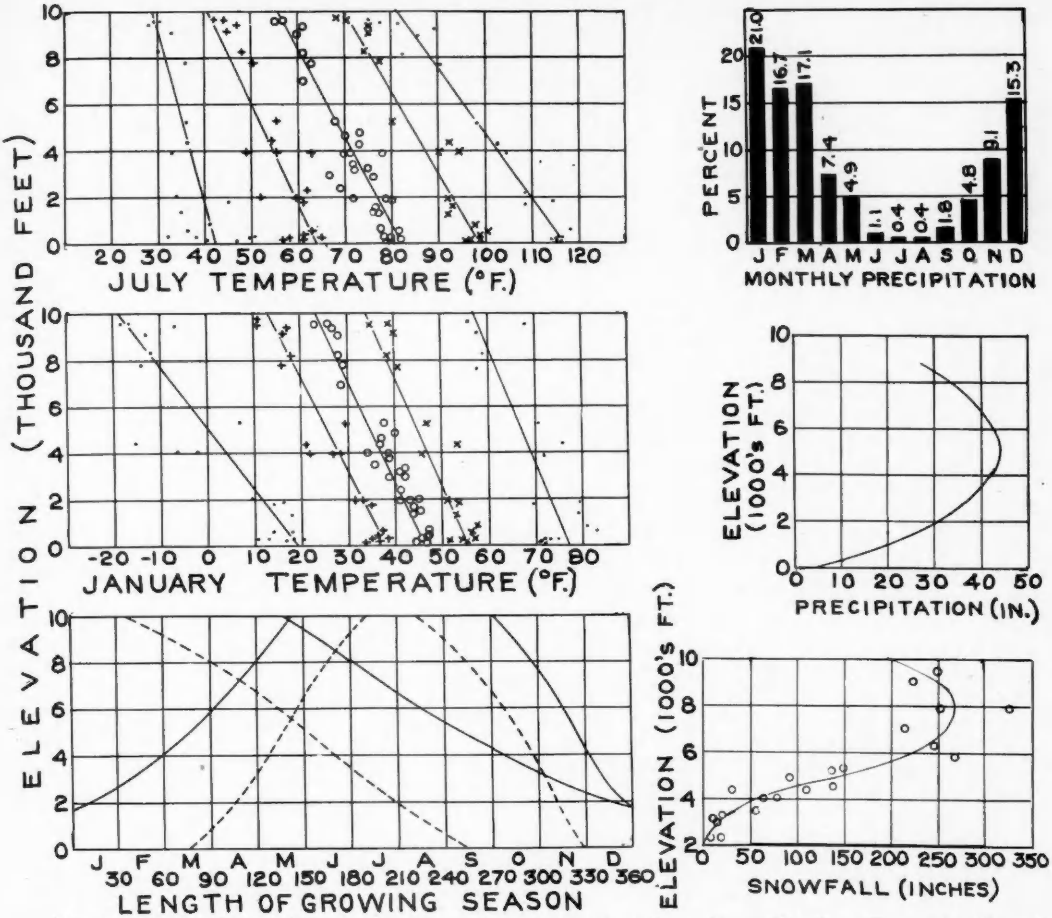

FIG. 6. Climatic characteristics in Area 9, western slopes of southern Sierra Nevada. (For explanation of charts and symbols see page 227.)

it is some 50 miles from them. The climate at the lowest elevations is therefore quite variable, and the graph represents only an average. According to these graphs, the mountains of southern California are remarkably warm compared with the southern Sierra. In particular the mean minima are very high. The cause is probably the southern latitude, as well as nearness to the ocean. There may, however, be a systematic error here—one opposite to the error usually found in the mountains, for the number of stations on ridges is unusually great, and night-temperature inversions characteristic of valleys are not recorded. The minimum temperatures at Mount Wilson, the highest station, are remarkably high at all seasons. On the basis of all these records, the temperature lapse rate in these mountains appears unusually low—as little as 1.0 degree per 1,000 feet for July minimum temperatures.

The precipitation is believed to increase up to an elevation of about 8,000 feet in these mountains. The annual distribution pattern by months is based almost wholly upon stations on the west slopes. The desert-facing slopes have somewhat more summer rains and correspondingly less winter rain, but there are insufficient data for computing the amount of difference.[8]

AREA 11—EASTERN SLOPES OF CASCADE RANGE AND OKANOGAN MOUNTAINS

LOCATION AND TOPOGRAPHY

The east slopes of the Cascades in Washington are broad and complex, marked by long spur ridges from the main crest, between which lie the drainages of

[8] The irregularity of the rainfall in this area has stimulated an unusual amount of study. Varney (1925) determined the variability from year to year, and more recent work has dealt with variations within the season. Conroy (1933) shows that the early and midseason rains are considerably more dependable than those of the late season. Blake (1933) correlates this dependability with the origin of the rain-bearing storms. The dependable rains come in midwinter and have a north Pacific origin. Rains at other seasons are irregular: in February they are frequently heavy and come from the south Pacific; in late spring they tend to center in Nevada; and in the autumn heavy, unwelcome rains of Mexican origin appear. An early study of precipitation in this area by McAdie (1914) places the zone of maximum at 8,000 feet elevation.

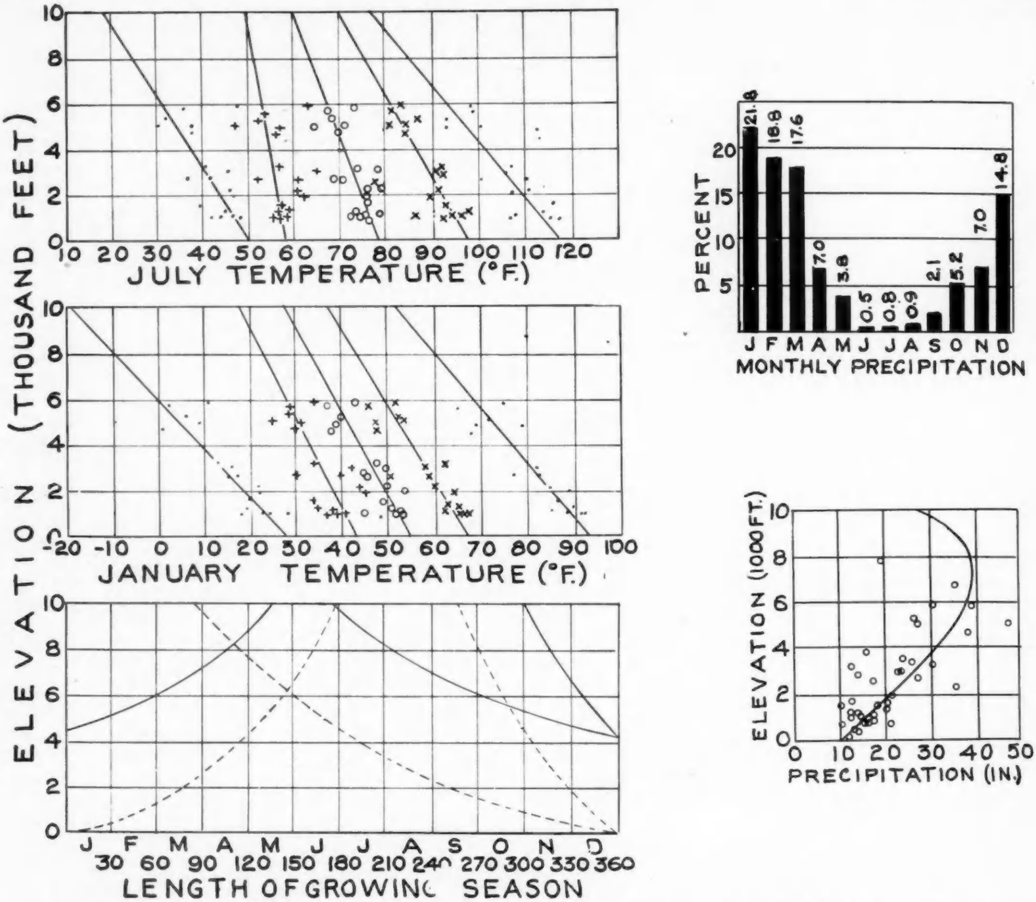

Fig. 7. Climatic characteristics in Area 10, southern California. (For explanation of charts and symbols see page 227.)

such large rivers as the Yakima, Wenatchee, Methow, and Okanogan, as well as Lake Chelan. East of the Okanogan River a series of poorly defined low north-south ridges extend to the Clark Fork of the Columbia, which marks the eastern boundary of this area.

Climatic Characteristics

Area 11 is one of great climatic diversity, especially with respect to rainfall, which, as on most lee slopes, is poorly correlated with altitude. In summer the temperature lapse rate is very rapid, owing to the high temperature of the low-level stations on the edge of the "desert" of interior Washington. The graphs have been drawn so that the temperatures at 6,000 feet elevation will agree with those on the charts of the windward slopes (Area 2). The area has been subdivided at the Okanogan River. To the west on the slopes of the Cascade Mountains the rainfall pattern is of the north Pacific type, very similar to that on the west side of the summit. East of the Okanogan River the monthly distribution pattern is very different, resembling that of northwestern Montana (Area 15). The annual precipitation is low here and is apparently little affected by changes in elevation. Summer thunderstorms are frequent.[9]

AREA 12—CENTRAL OREGON

Location and Topography

East of the crest of the Cascades, as considered in Area 4, relatively short slopes fall away to the Deschutes River. As there are no stations the climate of these lee slopes cannot be described. East of the Deschutes River the elevation increases again through a country that lies largely in the drainage of the John Day and Crooked Rivers to the Blue Mountains. These mountains lie on the divide between streams that flow into the Snake River and those that flow into the lower Columbia. They are moderately high

[9] Morris (1934), who has studied the incidence of lightning storms in this area, presents a map showing the number of storms per year per 100,000 acres. There is a stong concentration in the Okanogan Mountains.

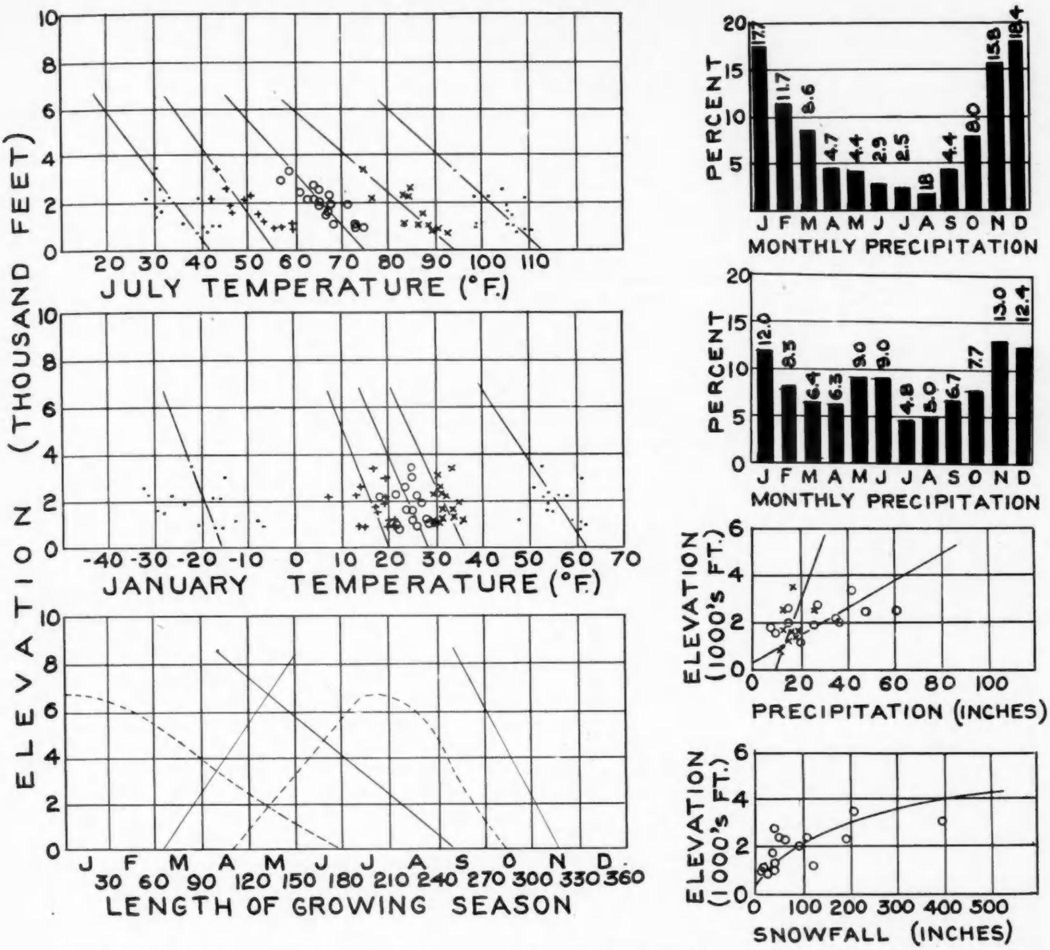

FIG. 8. Climatic characteristics in Area 11, eastern slopes of Cascade Range and Okanogan Mountains. (For explanation of charts and symbols see page 227.) Precipitation pattern charts: upper, slopes of Cascade Range; lower, Okanogan Mountains. Precipitation elevation chart: data for Cascade Range marked *o*, for Okanogan Mountains *x*.

(averaging about 8,500 feet elevation) and descend to the high plains of the Great Basin and Snake River (about 4,000 feet elevation) on the south and southeast.

The higher Wallowa Mountains in the extreme northeastern part of Oregon are separated from the Blue Mountains by the valleys of the Grand Ronde and Powder Rivers and appear to be more closely allied climatically to the north Idaho region (Area 14).

Climatic Characteristics

In this area—apparently one of transition—many of the climatic factors vary considerably with location as well as with elevation. The graphs represent rather crude averages, typical largely of the central part of the region. In temperature and pattern of rainfall distribution the area appears similar to northern Idaho (Area 14); but the amount of rainfall is much less and increases more slowly with increasing elevation. This fact doubtless accounts for the poorer forest growth and the prevalence of ponderosa pine. This region is better watered—elevation for elevation—in the northeasterly portion than in the west and southwest, which are in the rain shadow of the Cascade Mountains.

Though the rainfall pattern is somewhat similar to that of Idaho, it too varies with position and even with elevation. Westward the pattern resembles that on the west side of the Cascades, with wet winters and a single well-defined summer drouth. A similar type of rainfall occurs at high-altitude stations throughout central Oregon; but at lower elevations it resembles the Idaho type, with rather well-maintained rainfall through the spring months to June.

May is often as wet as many of the midwinter months. The accuracy of the graphs in these mountains is therefore low. Summer thunderstorms are frequent, as has been shown clearly in the study by Morris (1934).

AREA 13—UPPER KLAMATH-PIT-FEATHER BASINS

Location and Topography

On the headwaters of the Klamath, Pitt, and Feather Rivers, and on the slopes draining into the Great Basin as far south as Mono Lake, lies a region of relatively low rainfall in which is developed an extensive forest of ponderosa and Jeffrey pines. Most of the valley floors are at about 4,000 feet elevation; and the mountains are irregular, rising in general to no great heights above the valleys. It is locally known as the "east-side pine region." In a topographic sense, it extends south of the Mono region as a narrow, steep easterly slope of the Sierra Nevada. The climate of this narrow ribbon, being little known, cannot be considered here.

Climatic Characteristics

Since the climatological stations in this region are almost exclusively on the valley flats and plains, altitudinal trends cannot be worked out. In summer the temperature relationships resemble those of equal elevations on the west slopes of the Sierra Nevada; but the winters are distinctly colder, the means being about 5 degrees lower. The effects of altitude on rainfall appear to be local and are strongly masked by the great rain shadow of the Sierra Nevada and Cascade ranges to the west. In general there is a decrease eastward from the mountains out into the desert of southern Oregon and Nevada. Within the Klamath River drainage, the monthly distribution pattern resembles that of the mountains in central Oregon (Area 12). At the south end of the region, from the head of the Feather River to Mono Lake, it resembles that of the north Sierra Nevada (Area 8).

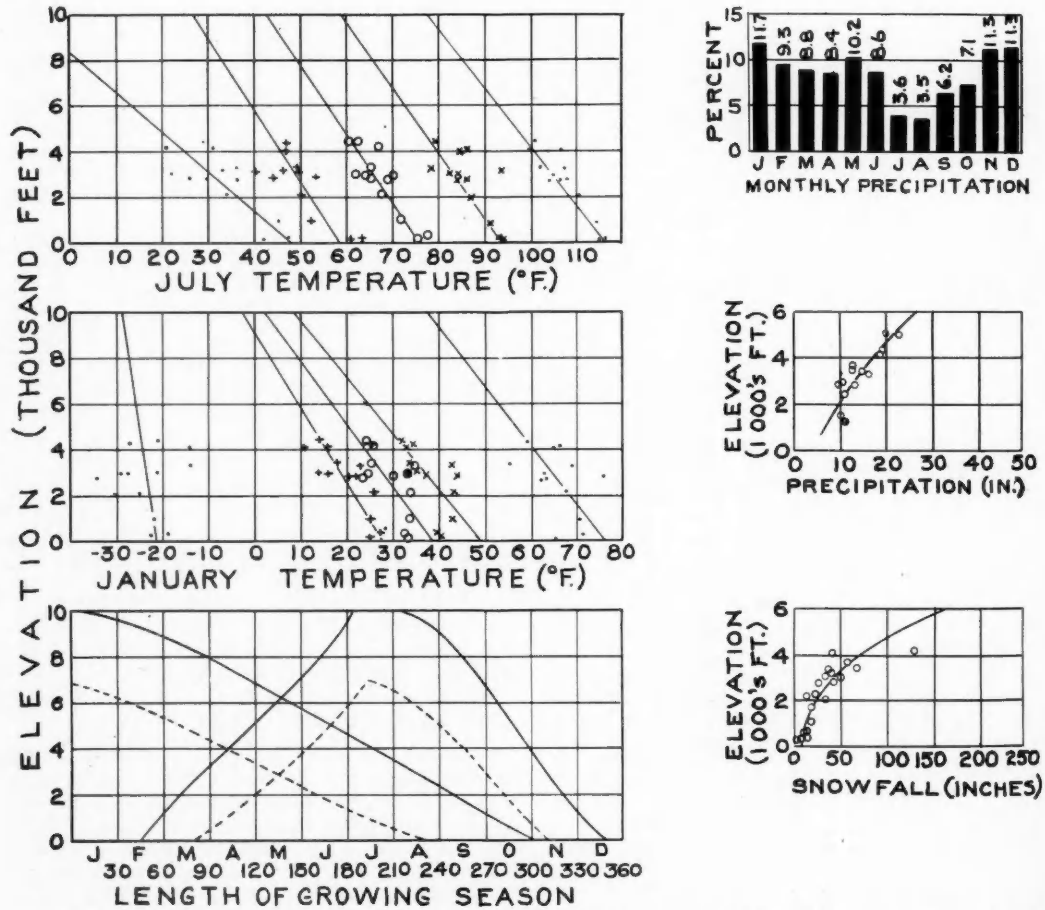

Fig. 9. Climatic characteristics in Area 12, central Oregon. (For explanation of charts and symbols see page 227.)

In the intervening region, largely in the Pit River drainage, there is an intermediate type, very similar to that noted in the southwestern part of Idaho (Area 17). This whole area is one of transition; and distinct climatic districts are difficult to set off, their boundaries being vague. Standard climatic maps are reliable for most of the region.

Average temperature characteristics on the valley floors at elevation of 4,000 to 4,500 feet elevation are as follows:

	July	*January*
Mean temperature	65	28
Mean maximum	85	39
Mean minimum	45	17
Highest observed	103	66
Lowest observed	25	—22

The growing season (above 42°F.) opens April 10 and closes November 1. Since the last frost in spring is about May 20 and the first in fall is September 20, the frostless season is about 120 days.[10]

AREA 14—NORTHERN IDAHO

LOCATION AND TOPOGRAPHY

This area consists of an intricately mountainous region rising from the semi-arid grasslands of interior Washington and adjacent Oregon and running eastward to the climatic divide, which undoubtedly coincides with the crest of the Bitterroot Mountains and associated ridges in line with them farther north. Toward the north lie the southern ends of some of the great trench valleys that extend far into British Columbia. Southward this region is usually cut off at the Salmon River or even at the southern limits of western white pine; but it seems wiser, in the present study, to include a lobe that extends across the Salmon and Snake Rivers into the Wallowa Mountains of northeastern Oregon.

CLIMATIC CHARACTERISTICS

This region is a humid island where the Pacific Coast forests of Douglas fir, grand fir, western red cedar, and western hemlock reappear in association with western white pine. This "white pine region" or "interior wet belt" of the Canadian ecologists has a rainfall resembling that of the east slopes of the Cascades in amount (Area 11), but considerably more evenly distributed through the year. Although well watered in a sense, it is subject to severe dry spells and to hot winds of low humidity from the "deserts" on the west, which make it one of the worst areas in all the country for destructive forest fires. The rainfall-altitude relations are not dependable, for the region consists of several ranges. The westernmost, open to the plains, are the best watered; eastward the precipitation diminishes except where the trend is neutralized by increasing elevation.

The temperature climate is locally affected to a striking degree by night temperature inversions, particularly in the broad, flat-bottomed valleys toward the north part of this area. Nearly all the climatic stations are in these valleys. Judging from work done in the Priest River Valley by Hayes (1941), the graphs presented here may well be in great error if they claim to represent temperatures on open slopes at the altitudes indicated. According to these studies of Hayes, the mean temperature for July may be as much as 10 degrees too low in these graphs at lower elevations up to 4,000 feet, and the mean temperature may be some 5 degrees low; the mean maximum appears substantially correct. Presumably there are similar errors in the January graphs, but winter temperature inversions have not been studied for this region.[11]

AREA 15—NORTHWESTERN MONTANA

LOCATION AND TOPOGRAPHY

On the headwaters of the Clark Fork of the Columbia River, between the crests of the Bitterroot and Coeur d'Alene Mountains on the west and the main Rocky Mountains on the east, lies a region of great topographic diversity. It is marked by generally broad valleys having northwest-southeast trends, which are the southern ends of some of the great trench valleys better developed in Canada. These valleys are separated by the major mountains, running in long ridges with a similar trend and broken at intervals by cross valleys. The general level of the valleys is about 3,000 feet elevation, and the mountains rise generally 3,000 to 6,000 feet higher. Toward the southeast, the Continental Divide at the head of the drainage of the Clark Fork consists of low ridges and broad passes in which the divide is hardly noticeable. The northern boundary of this area is set arbitrarily at the Canadian border.

CLIMATIC CHARACTERISTICS

The climatic elements of this region can be read from maps that reflect the conditions on the valley flats at about 3,000 feet elevation. The average temperature climate is indicated by the following:

Temperatures	*July*	*January*
Lowest observed	32	—31
Mean minimum	47	14

[10] There is little literature dealing with the climate of this area. Varney (1920), however, shows that there is a slight increase in summer rainfall with decreasing elevation in the region from Truckee, California to Reno, Nevada. Lee (1911) shows the rate of decrease of rainfall on the leeward slopes of the Sierra Nevada in the Owens Valley region, which is farther south than the area considered here. The graphs are, however, perhaps indicative of the decrease farther north.

[11] The importance of forest fires and fire-weather in this region has stimulated several valuable studies of mountain climates by foresters. The work of Hayes (1941), already cited in the text, involved a study of the summer climate of the Priest River valley showing the strong night temperature inversions and the resulting effects upon relative humidity and fire danger. More general studies had been made earlier. The temperature records at several high-elevation lookout stations were reported by Larsen (1922). Judging from fragmentary data, the summers are several degrees warmer than is indicated by the graphs in the present publication. Larsen and Delevan (1922) concluded that a monthly precipitation of 2 inches spelled comparative safety from forest fires. Larsen (1925) also determined the decrease of temperature with elevation. The temperatures shown in his graphs are considerably higher than those given here, apparently because he used stations that were relatively free from temperature inversions. Henry (1919) discusses two examples of increase of rainfall with elevation in this area. Haig, Davis, and Weidman (1941) have covered the climate of the western white pine region in some detail, but without adequately considering the changes that are caused by elevation.

Mean	65	23
Mean maximum	83	32
Highest observed	102	58

The growing season (temperatures above 42°F.) is April 15 to October 15, a period of 183 days. The frostless season is June 2 to September 10—100 days. This climate is approximately that indicated for northern Idaho (Area 14). The area here is much drier, however, with an average rainfall of about 21 inches and a snowfall of about 70 inches. Changes of climate with increasing elevation cannot be worked out in this region because the only stations are on valley bottoms. Presumably, conditions are like those in northern Idaho (Area 14).

The distribution of precipitation by months is highly variable, since this region appears to be one of transition. Toward the west the distribution resembles that of northern Idaho, with the winters distinctly wetter than the summers. The eastern edge is very different, for it lies next to the northern plains where rainfall is much heavier in summer than in winter. Although several transition types might be recognized, a simple, broad classification has been adopted with two subregions:

(1) the drainage of Clark Fork below the mouth of the Bitterroot River and

(2) the Flathead, Bitterroot, and upper Clark Fork Region.[12]

AREA 16—SOUTHWESTERN MONTANA

Location and Topography

East of the Continental Divide in southwestern Montana are several ranges and high ridges separated by broad grassy valleys along the headwaters of the Missouri River and its tributaries. The area is bounded by the montains of the Continental Divide on the west and south and by treeless plains on the

[12] The forest geography of this region has been studied by Larsen (1930), who selected several climatological stations in three different forest types and from them worked out the general climates. The climatic differences are more related to geographic position than to altitude. The precipitation is much affected by the position of rain shadows. Although the statistical basis is slender, the results appear dependable.

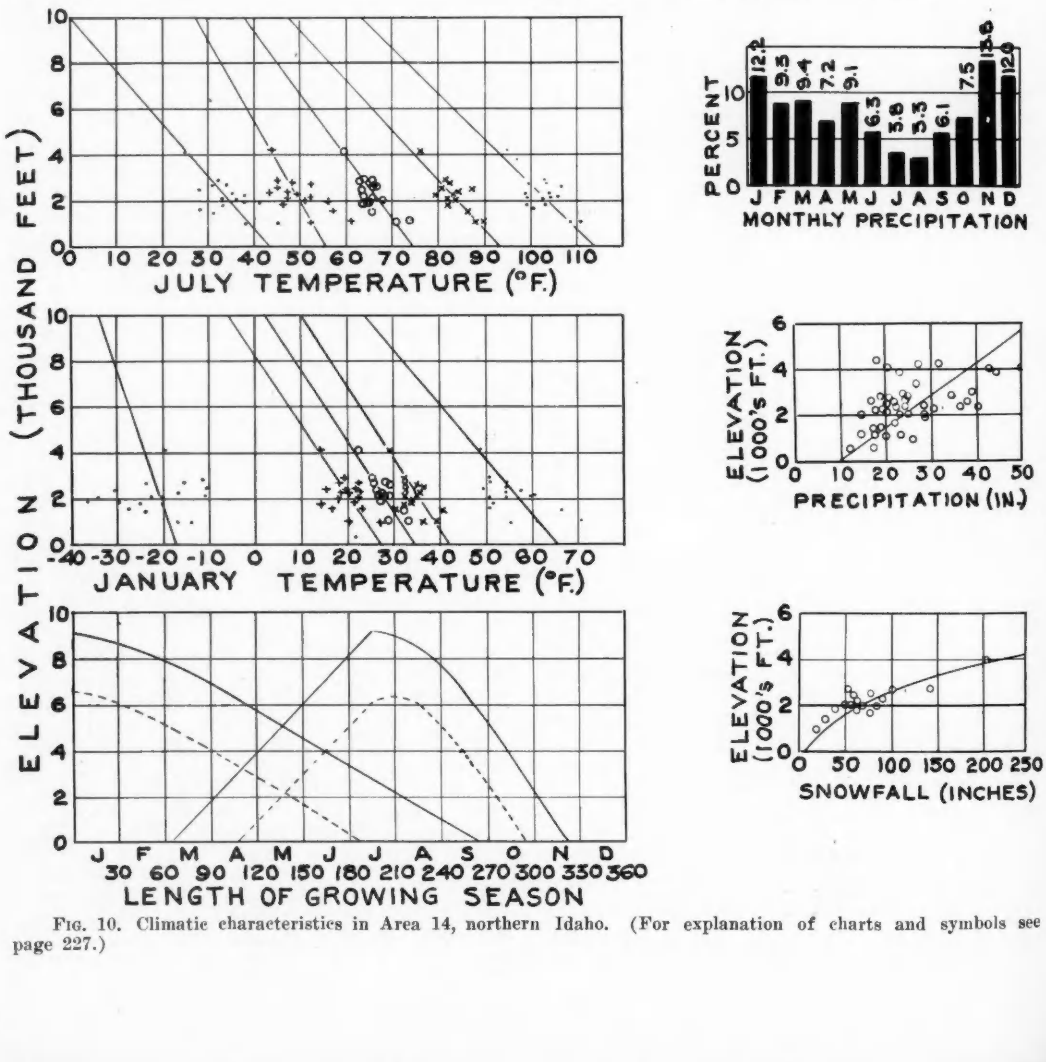

FIG. 10. Climatic characteristics in Area 14, northern Idaho. (For explanation of charts and symbols see page 227.)

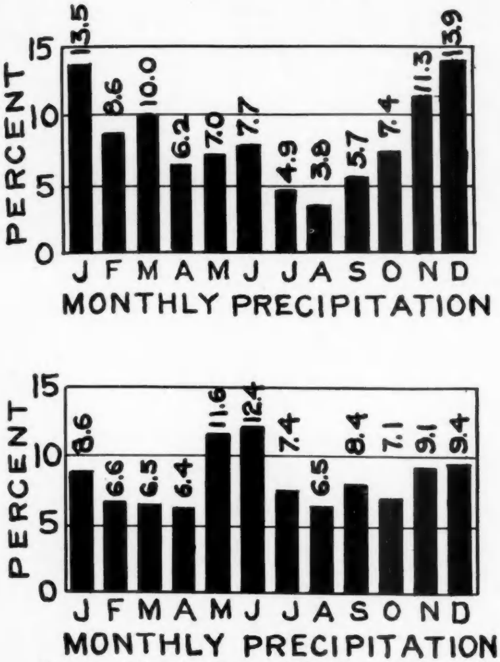

FIG. 11. Climatic characteristics in Area 15, northwestern Montana. Upper, distribution pattern in lower Clark Fork; lower, distribution pattern in Flathead, upper Clark Fork, and Bitterroot Valley region.

east. Climatological stations in the mountains of this region are rare; but a few, unfortunately concentrated in the southern section inside or near the Yellowstone National Park, have records from which one may construct rough altitudinal trend graphs.

Climatic Characteristics

In this region of low rainfall, the lower "dry" timberline lies at elevations as high as 5,000 feet. The rainfall pattern is of a well-developed "plains type," with relatively heavy precipitation in May and June. The increase of precipitation with elevation appears remarkably small—only about 2.5 inches per 1,000 feet. The temperature climate recalls that of western Wyoming, to the south; but the similarity may be more apparent than real, because the mountain stations are mostly in the southern part. Probably the readings shown by the graps are somewhat higher than the average of the region, provided temperature inversions do not mask the trends too greatly.[13]

AREA 17—CENTRAL IDAHO

Location and Topography

South of the Salmon River in Idaho lies an immense mass of mountains, located for the most part on a great granite batholith that has been deeply cut by an intricate series of deep canyons draining north into the Salmon River or southward to the Snake River plains. This great area is marked by few well-defined ridges higher than their neighbors—except in the south-central part, where the Sawtooth Mountains rise well above the generally accordant ridge crests of the major part of the uplift. In this wild and thinly populated country, climatological stations are few.

Climatic Characteristics

If one reads the graphs literally, this area is marked by a climate of greater extremes than are noted elsewhere in the west. The diurnal temperature range in July is about 40 degrees F.—higher than in any other area found in this study. The annual range in mean temperatures from January to July is 45 degrees, which is equalled, but not exceeded, in several other areas. The diurnal range of temperatures generally increases here with elevation, instead of decreasing as one might expect. Unfortunately there is much reason to doubt the accuracy of these observations, for the stations are few and poorly located. Most of them lie along the southern edge of the mountains from Weiser to Mackay, slowly increasing in elevation toward the east with the rise of the Snake River plains. The "continentality" of the region appears to increase eastward in the direction of increasing elevation. Altitudinal effects therefore become confused.

The rainfall is scanty and differs both in amount and distribution in two sub-areas that have been recognized. In the south part the division between these two regions of differing rainfall lies, rather clearly, at the Sawtooth Mountains. Farther north, where there is no well defined "backbone" range, the place and nature of the transition are unknown.

AREA 18—BASIN RANGES OF NEVADA AND WESTERN UTAH

Location and Topography

This wide area is characterized by elevated desert valleys and plains at 4,000 to 5,000 feet above sea level, from which rise many abrupt mountain ranges having a north-south trend. The crests of these ranges vary in elevation to a considerable degree, but the highest commonly exceed 10,000 feet.

Climatic Characteristics

Climatic data here are very scanty and are available only for valley stations. No altitudinal trends can be determined. The temperature climate in the valleys apparently resembles that of Utah at equivalent elevations, and most likely the rate of decrease with elevation is also similar. The distribution of forest types strengthens this probability.

The rainfall is scanty—5 to 10 inches a year except near high mountains. In particular the Ruby Mountains, the Deep Creek Range of the east border of Nevada, and other mountains in that part of the state are extensive enough and high enough to bring

[13] Larsen's study (1930), described more fully in footnote 12, applies to portions of this area also.

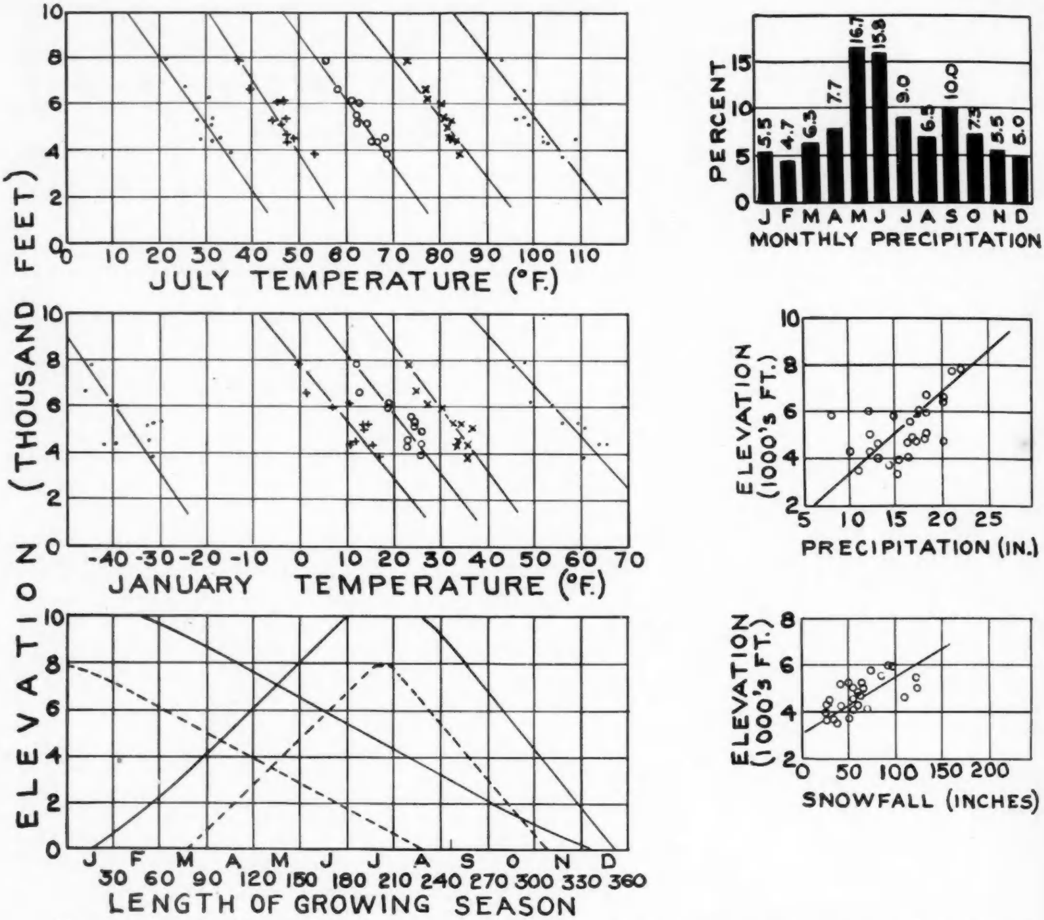

FIG. 12. Climatic characteristics in Area 16, southwestern Montana. (For explanation of charts and symbols see page 227.)

about 15 to 18 inches of precipitation at their windward bases. Judging from the amounts of snow present in spring, precipitation increases with elevation fully as fast as in the Utah mountains. In the western third of Nevada, where the mountains become lower and lie more in the great rain shadow of the Sierra Nevada, the increase of rainfall with elevation is probably less rapid.

Four broad rainfall patterns can be distinguished here, each essentially resembling the pattern in nearby regions that are considered elsewhere in this paper. In northwestern Nevada the distribution resembles that of the central Oregon area (Area 12); in the northeastern part it is like that of central Idaho (Area 17B). From Wyoming to the south Sierra Nevada in an extensive and arid region running through the middle of Nevada, the pattern is loose; stations close together vary a great deal. The general average is close to the pattern in western Wyoming, with a fairly even monthly distribution. Farther south the influence of the Arizona type of rainfall begins to be felt, and the south Utah pattern is closely approached.

AREA 19—WESTERN WYOMING

Location and Topography

In the northwest corner of Wyoming lies the Yellowstone Plateau, from which radiate many high mountain chains. Toward the south runs a range that faces the lava plain of southern Idaho on the west and falls away to the high basin of the upper Green River on the east. Still farther east lie the Wind River Mountains, whose western slopes are also included in this area. Their climatology is, however, so little known that the graphs may not accurately represent conditions on these slopes.

Climatic Characteristics

Most of the stations that serve as a basis for the graphs given here are in the mountains near the

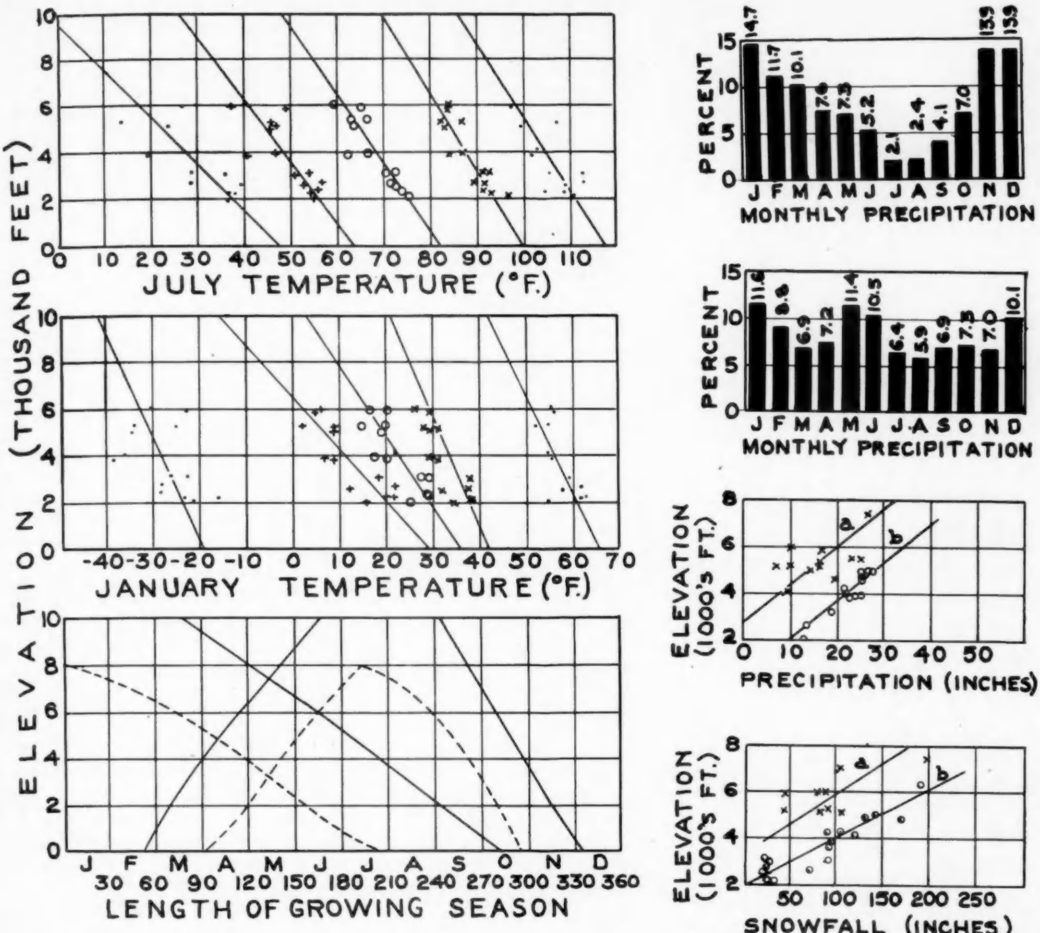

FIG. 13. Climatic characteristics in Area 17, central Idaho. (For explanation of charts and symbols see page 227.) Precipitation pattern charts: upper, western half of area; lower, eastern half of area. Precipitation and snowfall charts: Curves *a*, eastern part of area; curves *b*, Boise, Payette, and Weiser River drainages.

Idaho-Wyoming line. Because the Snake River plains at the west base of these mountains become very hot in summer, the temperature lapse rates are remarkably high in both summer and winter—approaching 5 degrees F. per 1,000 feet. Temperature inversions in the flat valleys of the plateau tops perhaps also contribute to this result.

The distribution of rainfall by months in this area is more even than in any other part of the west covered in this study. Essentially the same pattern extends far to the southwest across Nevada almost to the Sierra Nevada.

AREA 20—CENTRAL WYOMING

LOCATION AND TOPOGRAPHY

In north central Wyoming lies a large area of mountain and plain drained by the Big Horn River and its tributaries. The western side of this drainage consists of mountain spurs jutting out from the Continental Divide and developing an area of rough, steep mountains cut by deep canyons. The largest of these ridges, the Shoshone Mountains, with their continuation the Owl Mountains, run almost to the Big Horn River and almost cut the basin in two. The east and south boundaries of the Big Horn drainage are marked by low hills and high rolling sagebrush plains except where the isolated Big Horn Mountains rise from the valley plains (5,000 to 6,000 feet elevation) to altitudes of 10,000 feet and more.

CLIMATIC CHARACTERISTICS

The temperature climate closely resembles that of Area 19, immediately to the west, except that the lapse rates are much less rapid, being close to the general averages. This difference appears to result largely from the warmth of the high-elevation mountain stations in this central part of the state. Valley

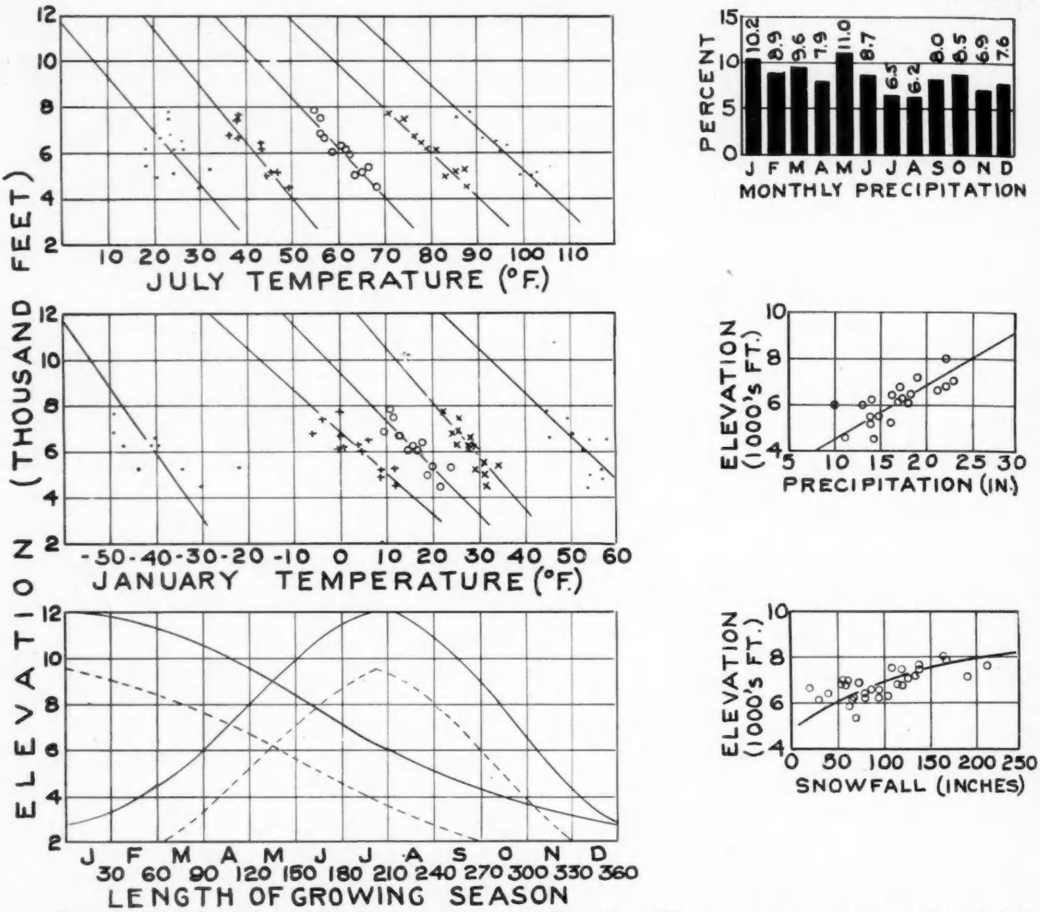

FIG. 14. Climatic characteristics in Area 19, western Wyoming. (For explanation of charts and symbols see page 227.)

temperatures are like those on the Snake River plains. The warmth of the mountain stations is probably due to less pronounced temperature inversions, better air drainage, and also chinook effects (particularly in winter).

This area has a very dry climate, especially near the west base of the Big Horn Mountains; and the distribution pattern differs sharply from that in western Wyoming, having a sharp maximum in May. Though the position of the line separating these two rainfall regimes is uncertain, it is assumed to be near the crest of the Wind River Mountains.

AREA 21—UINTA MOUNTAINS

Location and Topography

In southern Wyoming and the adjacent parts of Colorado and Utah is a large elevated region marked by the Uinta Mountain Range, which lies in its southern portion. This range is the only large and lofty mountain mass in the west that is developed on an east-west axis. Near its eastern end it is cut through by the Green River, which flows in a deep canyon and the whole area falls into the Green River drainage. It is a region of scanty population and climatological data are too poorly distributed to permit computation of the altitudinal relations.

Climatological Characteristics

Virtually nothing can be said of the climate here. Presumably it differs somewhat on the north and the south sides of the Uinta Mountain mass and in general it doubtless resembles the climate of Utah and western Colorado. The rainfall pattern is probably one of very well-distributed precipitation, like the patterns of western Colorado (Area 23), Utah (Area 22), and western Wyoming (Area 19), which are adjacent.

AREA 22—UTAH

Location and Topography

The eastern and western parts of Utah are "desert"; but extending north and south through the

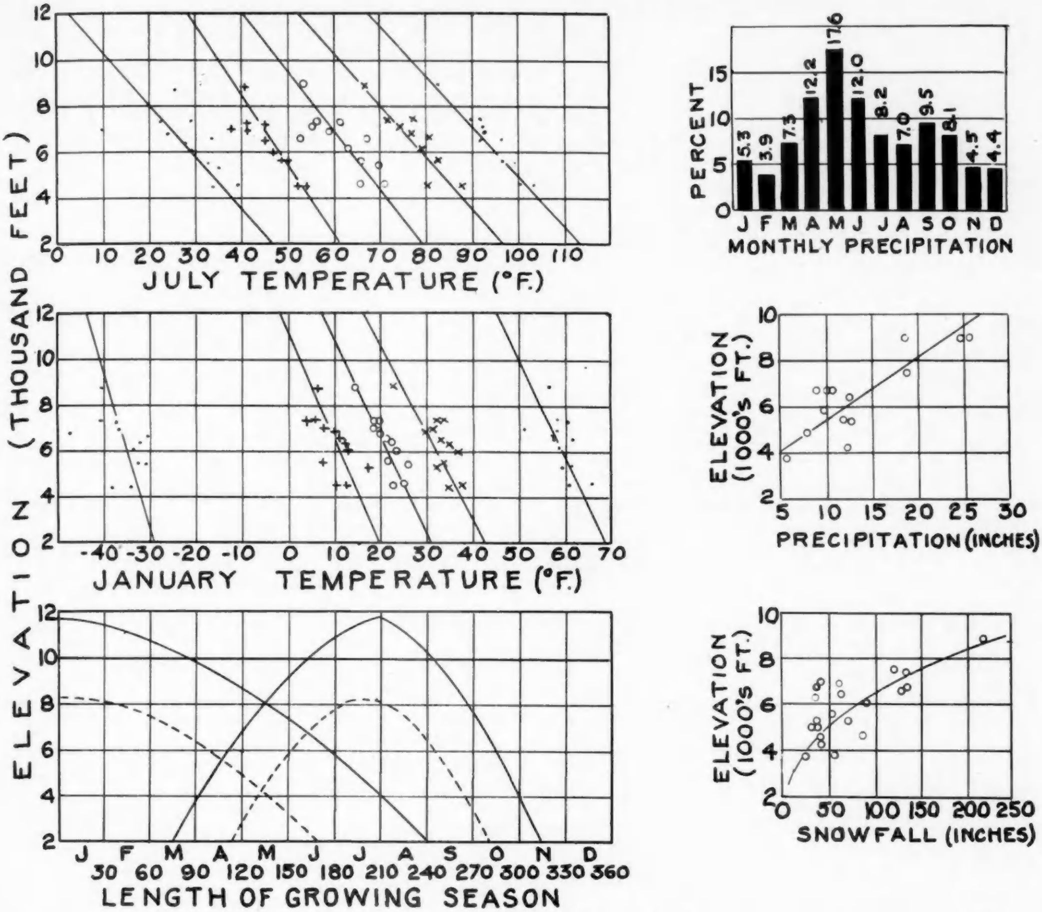

FIG. 15. Climatic characteristics in Area 20, central Wyoming. (For explanation of charts and symbols see page 227.)

central part of the state is a broken chain of mountains made up of several roughly parallel elements separated by rather broad valleys. Although these mountains are composed of several geologic types, from the sharp steep ridges of volcanic origin to the high plateaus of sedimentary rocks characteristic of southern Utah, they all culminate in crests that run generally as high as 10,000 feet, and they all have similar broad climatic aspects. The valley levels are about 4,000 to 5,000 feet in elevation.

CLIMATIC CHARACTERISTICS

The temperature climate of these mountains has no notable peculiarities. Though the annual range of temperature is somewhat above average, the lapse rates are near the general mean for the west. The rainfall distribution pattern is somewhat variable, for this is a region of transition, comprising three sub areas. Area 22A includes most of the chief mountains of the state, especially the west slopes that fall away to the more populous valleys. The pattern here is rather distinctive. In area 22B, from the latitude of Fillmore and southward, the Arizona-type influence is clear. In area 22C, lying on the east side of the mountain crests and falling away to the Colorado River, the pattern somewhat resembles that of western Colorado. In the whole Utah area, but especially area 22A, there is considerable difference between the pattern at valley stations and in the nearby mountains.[14]

[14] The lack of correlation between the rainfall at valley stations and the adjacent mountains has also been noted by Clyde (1931). His records, however, are short and fragmentary. Alter (1919) gives the annual precipitation on the west slopes of the central Utah mountains as 15 inches at 4,250 feet elevation and 30 inches at 8,000 feet on western slopes (somewhat more than shown by the graphs here) and 10 inches at 5,500 feet and 20 inches at 7,500 feet on eastern slopes—again, somewhat more than is indicated here. Price and Evans (1937) have reported on a series of four stations in central Utah that cover a difference of elevation of about 5,000 feet in ten miles. Since the stations are all situated where air drainage is good, there is little temperature inversion, and the values all run somewhat higher than in the present graphs.

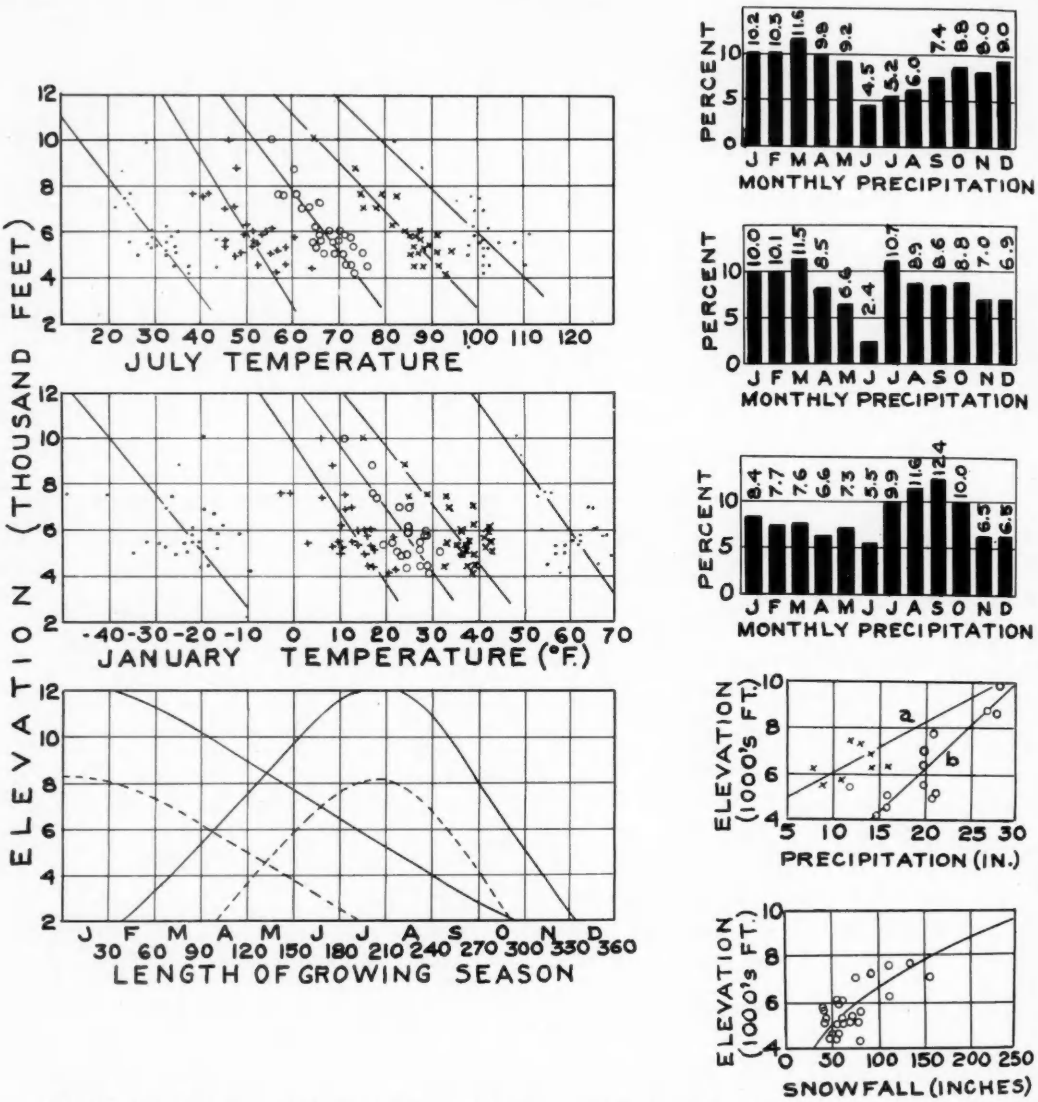

Fig. 16. Climatic characteristics in Area 22, Utah. (For explanation of charts and symbols see page 227.) Precipitation pattern charts: upper, Great Basin drainage, northern half of state; middle, Great Basin and Virgin River drainages, south half of state; lower, Colorado River Drainage. Precipitation—elevation chart: curve *a*, Colorado drainage (easterly); curve *b*, Great Basin drainage (westerly).

AREA 23—WESTERN COLORADO

Location and Topography

In western Colorado lies a broad region of mountains and plateaus, having an intricate topographic pattern and doubtless, an intricate climatic pattern—especially as regards precipitation regimes. Despite the adequate number of stations, the data are still too scanty to allow the breakdown of this region into smaller areas with well-defined climates.

The area used as a basis for the graphs shown here is the same as that included in the "West Colorado" area of the Climatological Summaries of the U. S. Weather Bureau—the portion of the state west of the Continental Divide plus the upper Rio Grande Valley. It is doubtful whether the Continental Divide and the Sangre de Cristo and Culebra Ranges represent the climatic divide more accurately or correctly than some of the nearly parallel ranges farther west—the Park Range, Saguache Mountains, and other uplifts. The area as defined, however, is made up of many diverse elements—the

high ranges in several ranks near the continental crest, the high valleys represented by Middle and San Luis Parks, the high bastion of the San Juan mountains off to the southwest, the deep canyon-cut country of the Colorado and Grand Rivers, and the plateaus toward the west edge of the state. No simple description can adequately characterize this region.

Climatic Characteristics

The climate of western Colorado as represented in these graphs can hardly apply accurately to all parts of such a diverse area. Specifically the broad high valleys or "parks" are subject to marked temperature inversions, especialy in winter; elsewhere good air drainage produces warm sites, notable for their fruit production. The precipitation climate is also variable. The slopes of the San Juan Mountains facing the Colorado desert in the southwestern part of the state are rather well watered for their elevation. The parks, pocketed between high mountains, are unusually dry, especialy the upper San Luis Valley. The percentage of the rainfall in each month is also somewhat variable; in the southern part of the state in the Rio Grande Valley and on the headwaters of the San Juan River and its tributaries there is some resemblance to the northern New Mexico type of rainfall; indeed that graph should perhaps be used in this locality (see Area 25).

The general climate of western Colorado has few peculiarities. It is colder than the slopes at equal elevation on the eastern side of the mountains (Area 24), probably owing to the greater stores of snow and the absence of chinook winds. Because many of the stations lie in valleys with poor air drainage, the correlation of minimum temperatures with elevation is singularly poor.

The rainfall is relatively well distributed throughout the year, and its pattern closely resembles that on the east side of the Wasatch Mountains of Utah. Rain shadows are not strikingly developed on either east or west sides of the major mountain ridges, a fact indicating that the rain-bearing winds come from either the east or the west.[15]

AREA 24—EASTERN COLORADO

Location and Topography

Compared with the "western slope" of Colorado, the eastern slope from the Continental Divide, the Sangre de Cristo Range, and the Culebra Mountains to the grassy western plains is relatively simple and abrupt, the width of this belt being 50 to 75 miles. Within this zone, however, are many ridges and local uplifts; there is no simple sweep from the plains to the crest. Two of the great "parks" lie in the high country near the divide—North Park and South. Mountain-crest elevations are generally high, 12,000 feet and more being common; and the easterly bases meet the plains grassland at 5,000 to 6,000 feet. Most of this area lies in the drainage of the Platte and Arkansas Rivers.

Climatic Characteristics

The climate here is without striking peculiarities demonstrable by these graphs. Owing to lesser amounts of snow and to chinook winds the winters are warmer than on equivalent western slopes of the range. In the high valleys, temperature inversions are so common and severe that the elevation has little bearing on the minimal temperatures.

Though the increase of rainfall with elevation is somewhat less rapid than on the west slope, there is great variability in rainfall, and the correlation is not too well established. This region has an unusual number of stations at mines and mining communities, often on slopes and ridges above the level of temperature inversions; hence the temperature graphs are unusually free of error from this cause.[16]

AREA 25—NORTHERN NEW MEXICO

Location and Topography

Around the head of the drainage of the Rio Grande in southern Colorado lies several ranges that extend southward on both the eastern and the western sides of the river through all the northern half of New Mexico. The valley between them is broad and has an elevation of about 6,000 feet, falling from north to the south. From this plain the mountains rise rather irregularly, some chains and knots having 11,000 to 12,000 feet elevation, especially in southern Colorado. Apparently the graphs given apply fairly well over all this area, though there is some doubt whether they surpass those of western Colorado (Area 23) for the section in the upper part of the San Luis Valley. They are probably safe to use as far north as La Veta Pass and through Archuleta and Conejos Counties.

Climatic Characteristics

There are few marked peculiarities here. The lapse rates of temperature are not far from average, but, as in Arizona, the annual range of temperature is smaller than farther north, indicating a relatively warm winter rather than unusually cool summers. Because of the broad flat valley with poor air drainage, temperature inversions are marked; the lowest temperatures, and even the mean minima, are seldom correlated with altitude.

[15] Robbins (1937) has extensively studied the vegetation and climate of Colorado and gives incidental material on the relation of climatic factors to elevation. He determined temperature lapse rates from the averages of 20 paired stations, each pair on the same watershed, and found them to be somewhat lower than in the present graphs—about 1 degree per 1,000 feet in January and 3 degrees per 1,000 feet in July. In comparison with the present figures, the frostless season at various elevations, as given by Robbins, runs 10 to 15 days shorter, while the increase of rainfall—2.4 inches per 1,000 feet—is higher. Hart (1937), on the other hand, presents graphs on the last point that agree very well with those given here except for the Fraser River drainage.

[16] The work of Robbins (1937) on vegetation and climate in Colorado, more fully mentioned in footnote 15, applies to this area also. In addition the study of Bates (1924), centering on a chain of stations in the Pikes Peak region, gives more specific information for that locality. Like Robbins, Bates finds a summer lapse rate of temperature of only about 3 degrees per 1,000 feet, whereas in the present paper it is about 3.7 degrees.

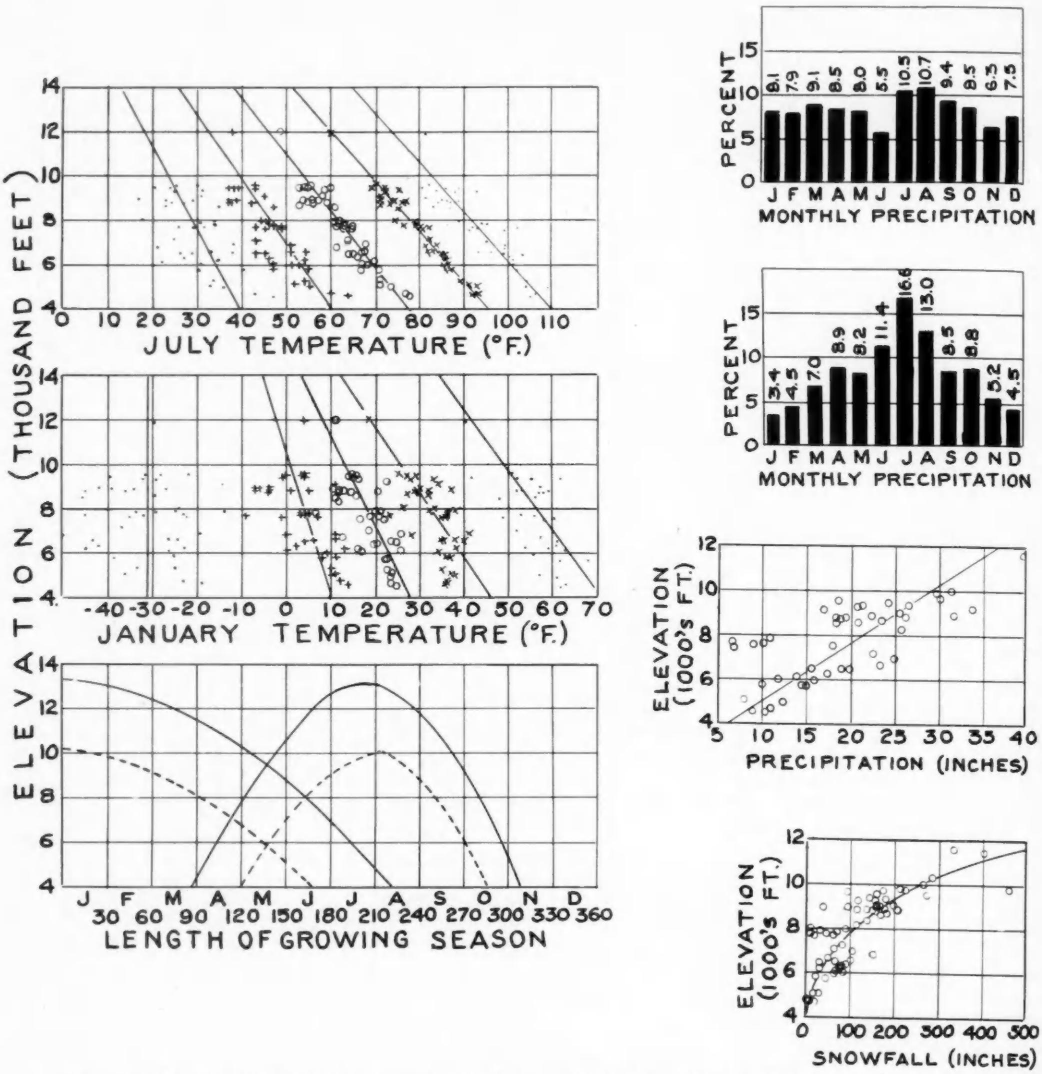

Fig. 17. Climatic characteristics in Area 23, western Colorado. (For explanation of charts and symbols see page 227.) Precipitation pattern charts: upper, all area except San Juan and upper Rio Grande drainages; lower, San Juan and Rio Grande drainages.

Considering their elevation, the valley stations, many of them flanked on both east and west by high mountains, are very dry. The precipitation pattern is uniform over the area and is marked by a heavy July rainfall, as in Arizona; but the June rainfall is less strikingly deficient than in that region.

AREA 26—ARIZONA

Location and Topography

Discussion of the mountain climates of Arizona must be limited mainly to the broad Colorado Plateau that extends from the rim of the Grand Canyon of the Colorado southward to about the middle of the state and thence eastward to the border of New Mexico. Although there are considerable mountain masses in other parts of the state, the altitudinal trends of climates are in general impossible to determine, because of the lack of sufficient stations. The Colorado Plateau is no simple flat table-land, but is much broken by eroded valleys and local volcanic uplifts. It presents, however, a fairly uniform climatic picture.

Climatic Characteristics

The southern position of this area apparently brings it beyond the zone effectively cooled in winter by the cold polar continental air, masses of which

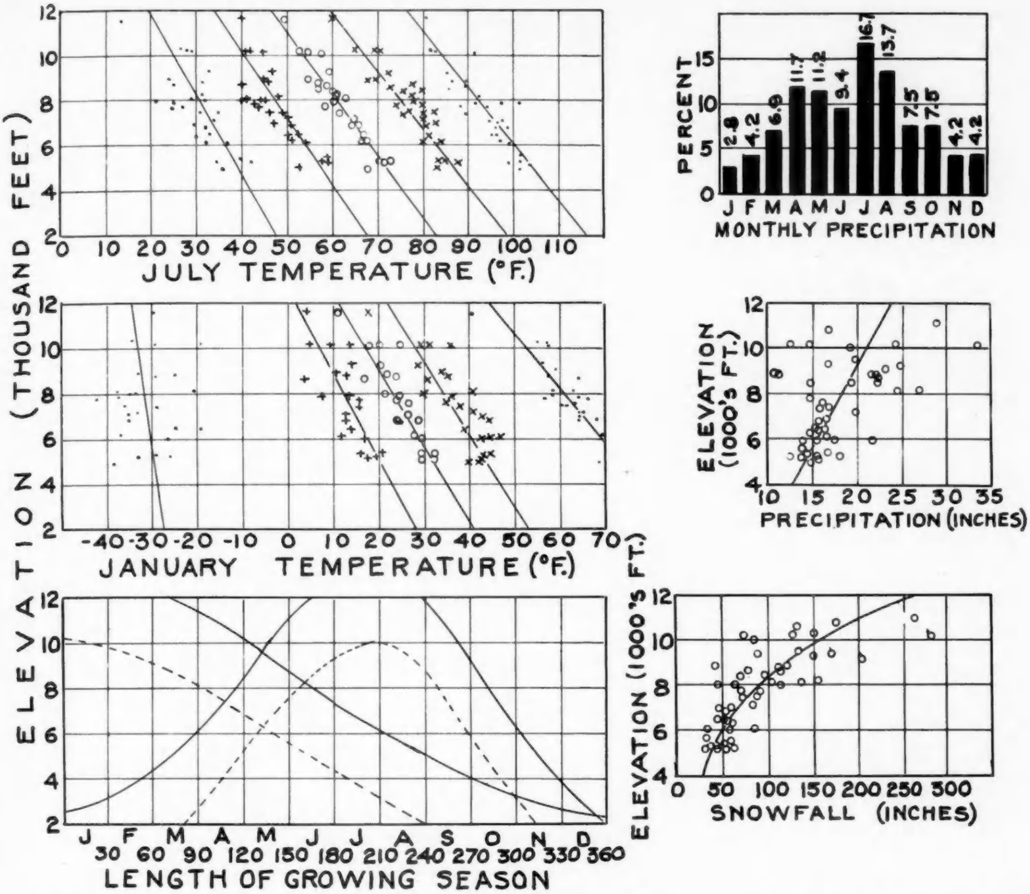

FIG. 18. Climatic characteristics in Area 24, eastern Colorado. (For explanation of charts and symbols see page 227.)

originate in the northern interior of the continent and flow outward. The winters are therefore distinctly warmer than in Utah and Colorado at equal elevations. In January and July the range between mean temperatures is only about 36 degrees F., whereas farther north it generally exceeds 40 degrees. The rainfall is usually scanty and comes in a typical pattern, with June very dry and July-August the wettest part of the year.[17]

AREA 27—SOUTHERN NEW MEXICO

LOCATION AND TOPOGRAPHY

This area contains two distinct bodies of mountains, separated by the valley of the Rio Grande. To the west they lie on the headwaters of the Gila River and the mountains marking the edge of the plateau region that stretches north and west into Arizona. The continuity of the plateau surface is here greatly broken by deep canyons and considerable volcanic activity, whereby a rough, steep country has been developed in many places, though the elevations are not great. Eastward from the Rio Grande, the divide between that drainage and the Pecos to the east is generally low; but the Sacramento Mountains and associated ranges are high enough to modify the climate. Though the mountains on the opposite sides of the Rio Grande are separated by a hundred miles of grassy plains, their climates appear essentially similar.

CLIMATIC CHARACTERISTICS

In southern New Mexico even more than in Arizona, the effects of a southern position are evident. The annual range of mean temperatures is unusually small—some 30 degrees F., as in the mountains of

[17] Pearson (1931) has studied the climate of the forested zones of the mountains of Arizona and New Mexico very thoroughly, presenting far more detailed information than is available in the present graphs and including such items as soil temperature and moisture. As regards temperature and precipitation, there is good agreement between the two papers; but Pearson shows that the temperature lapse with altitude does not make a straight-line curve in this region of elevated plateaus. Some of the data in the present publication for high-elevation stations are taken from Pearson, since the points are not Weather Bureau stations.

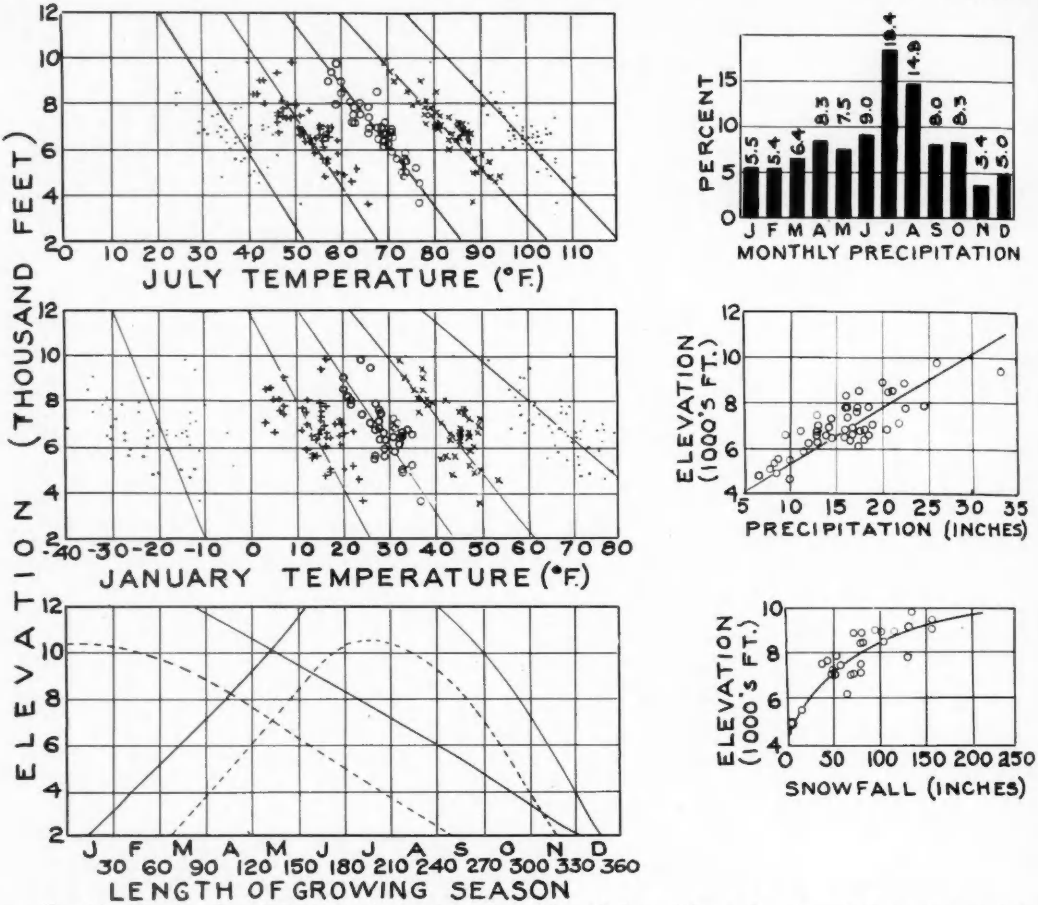

Fig. 19. Climatic characteristics in Area 25, northern New Mexico. (For explanation of charts and symbols see page 227.)

California. At low elevations the differences are somewhat greater than this because the region has a very high lapse rate of temperature in summer, a rather low rate in winter. The explanation is probably that the lowland plains are intensively heated in summer, while the mountains are cooled by the frequent local thunder showers and the accompanying cloudiness. The pattern of rainfall distribution is striking. Each month the precipitation from November until May of the next spring is a little less than 5 per cent of the annual rainfall. During the rest of the year the rainfall is much heavier, with a striking maximum in July and August.[18]

AREA 28—MEXICAN BORDER

Location and Topography

In the southern part of Arizona and adjacent New Mexico are several short mountain chains, some rising to considerable elevations. There are no satisfactory climatological stations at sufficient elevations to reveal much about the climate.

Climatic Characteristics

In many respects these mountains appear to resemble those of southern New Mexico (Area 27).[19]

APPENDIX A

Computation of the Mean Temperature in Months other than January and July

To show the whole annual march of temperatures by months at all elevations would require far more space than is available. Such data, if required, can be computed rather expeditiously with the aid of

[18] The publication by Pearson (1931), mentioned more fully in footnote 17, covers this region as well as Arizona. Krauch (1939) made a local study of the precipitation at Cloudcroft, at an elevation of 8,650 feet in the Sacramento Mountains; he gives, in addition to the usual figures, a compilation of the plus-and-minus deviations of rainfall through the 36-year period.

[19] Shreve (1915) carefully analyzed some rather fragmentary data collected in a few seasons in the Santa Catalina Mountains, indicating that these mountains are about 15 degrees warmer in summer than the ranges included in Area 27. The frostless season appears to be about the same, and the precipitation is of the same order. Smith (1910) has also investigated this last point; the rate of increase of precipitation with altitude given by him is the same as in the present graphs for Area 27, southern New Mexico.

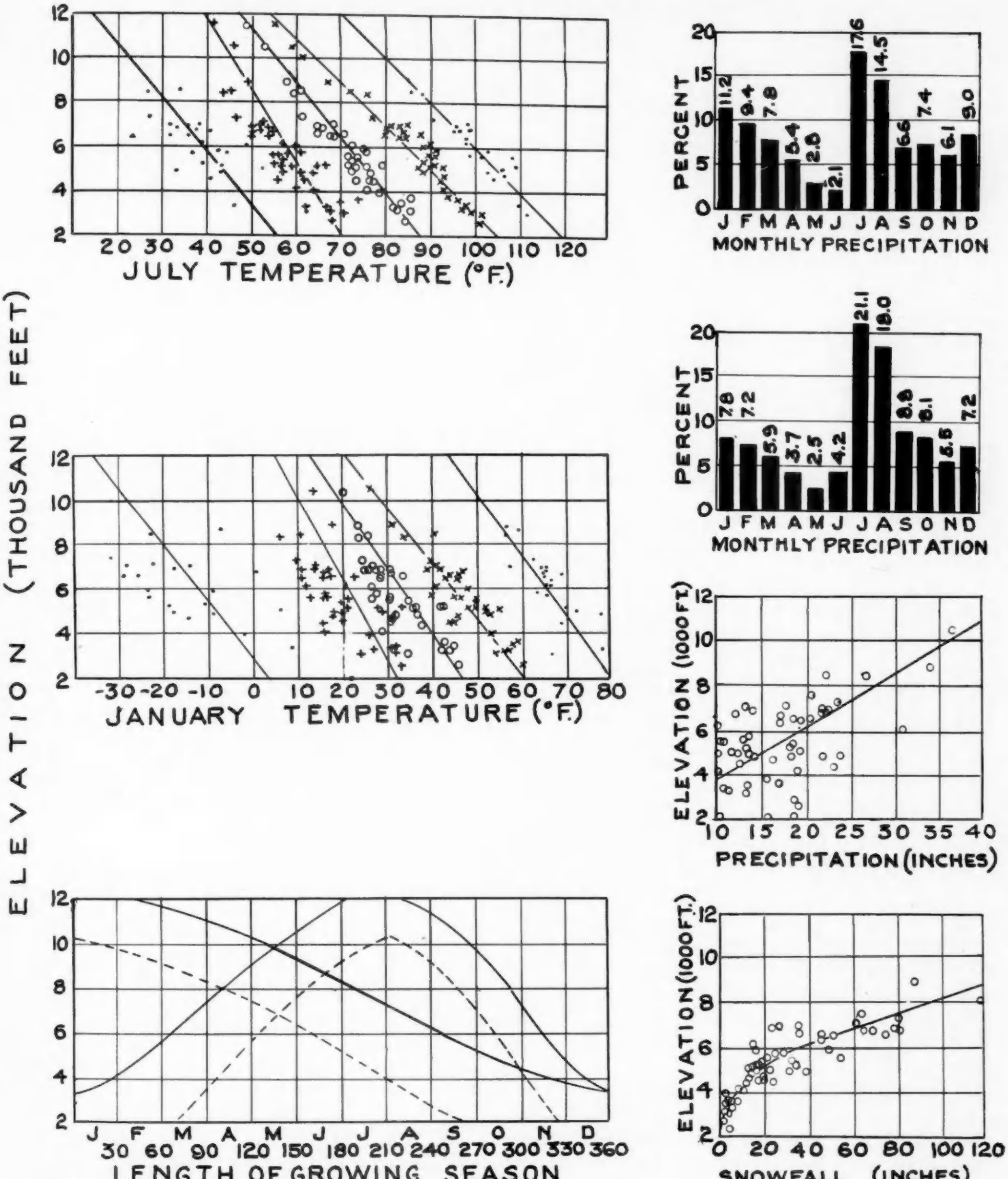

FIG. 20. Climatic characteristics in Area 26, Arizona. (For explanation of charts and symbols see page 227.) Precipitation pattern charts: upper, central and western Arizona; lower, eastern Arizona.

Table 1, for the march of temperature follows a fairly constant pattern over large areas and at all elevations—with certain exceptions that will be noted presently. In this table are given the temperatures that would appear if the January temperature was 0° and the annual range—the difference between the January and July means—was 100°. The values in the table simply need to be corrected—first, to fit the observed differences between the July and January temperatures for the place in question, which may be read from the appropriate graphs in the body of the text; second, to fit the observed January temperature of the place. An example will make this clear.

Suppose that the January mean temperature at a given elevation is read as 28°, the July temperature

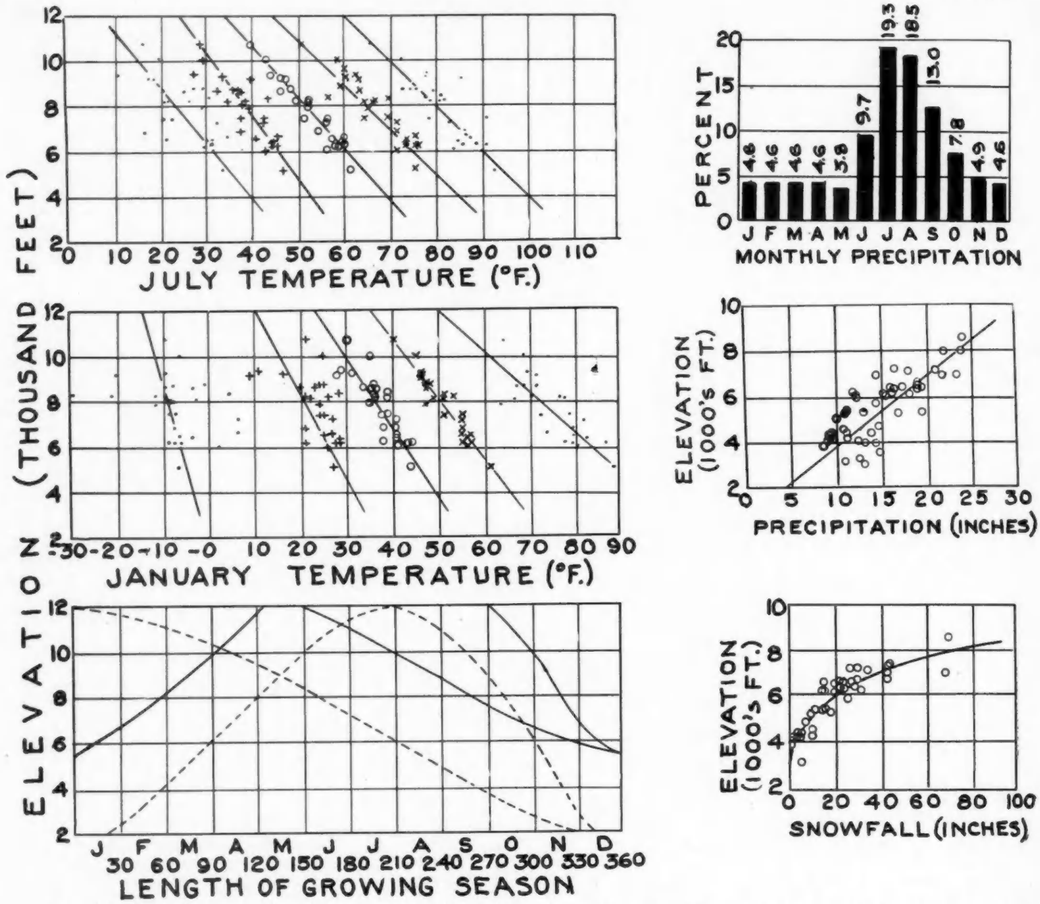

FIG. 21. Climatic characteristics in Area 27, southern New Mexico. (For explanation of charts and symbols see page 227.)

is 64°, and one wishes to compute the May temperature. Assume that the place is in Area 12. The difference between the January and July temperature is 36 degrees, not 100, so that the May temperature will not be 65, as shown in the table, but $\frac{36}{100}$ x 65 or 23.40. Since, however, the January temperature is not 0° but 28°, 28 must be added to the 23.4, giving 51.4 as the mean temperature in May. For careful work one should make local studies of the march of temperature at the nearest Weather Bureau stations and apply the figures so obtained to the case in hand. But for broad generalizations, these averages appear fairly accurate.

The temperature-march pattern is usually thought to vary with elevation in all regions where there is much winter snowfall, since the accumulations of snow in the mountains greatly delay the advent of spring. This delay appears rather well marked in the Cascade Mountains of Washington and Oregon, where the snow depth increases greatly with elevation. It is vaguely apparent in California, but seems too inconsequential to be recognized in this tabulation. Elsewhere it cannot be detected with any certainty, so

TABLE 1. Pattern of the march of monthly mean temperature through the year, developed by assuming the January mean temperature as 0 and the July temperature as 100.

Area numbers	"Relative temperature" for the months as shown								
	February	March	April	May	June	August	September	October	November	December
2*, 4*, 5, 13	12	25	43	61	81	98	78	52	27	6
2*, 4*, 8, 9	7	18	33	54	79	98	76	50	24	6
10	7	15	28	47	78	98	82	58	28	6
11	11	33	54	71	86	98	76	54	28	7
12, 14, 15, 16, 17	6	27	48	65	82	97	75	51	27	5
25, 26, 27	11	25	45	67	91	96	82	53	23	2
19, 20, 22, 23, 24	6	24	45	66	85	97	78	53	27	5

*In areas 2 and 4 use the values in the upper line for low elevations (up to 3,000 feet) and the values in the second line for elevations above 3,000 feet. Actually the upper values are average for about 1,000 feet elevation; the lower set for 4,500 feet. The basis for the high-elevation data is very scanty.

that the pattern of the general region is fairly representative of all elevations: certainly there is no well-defined variation of pattern with altitude. Minor differences appear between stations in the same region regardless of elevation.

APPENDIX B

The variability of the rainfall from season to season is recognized throughout most of the West as an important ecological factor affecting plant distribution. This variability is of course erratic; cycles of wet years may come and go, and at the same time individual years within the cycle may vary sharply from their neighbors. In such brief periods as a single month, the variability is even greater and more erratic. A general approach to the delineation of monthly variability of rainfall is given, nevertheless, in the following three tables. To use them one must know the mean or "normal" rainfall for the month in question. Then, by consulting Table 2, one may read the percentage of the time that the rainfall during that month is over double the normal. Table 3 shows the percentage of the time that the rainfall is less than half normal, and Table 4 the frequency with which no rainfall at all is to be expected. There is, to be sure, a considerable error in most of these tabulations because of the lack of a perfect correlation of variability with the normal rainfall in the month. At a certain place and normal November rainfall may be 2 inches and the June rainfall may be the same. The winter rainfall regime differs from the summer, and the assurance of rainfall of any specific degree in both months is by no means equal. Again, the June rainfall at 3,000 feet elevation in a certain area may be 2 inches, and the rainfall at 8,000 feet in August may also be 2 inches. To suppose that the certainty of rainfall in these two cases is governed by the same set of factors is very presumptive. In general, however, a surprising amount of constancy exists in these figures. The greatest errors are apt to occur in months when the rainfall is changing rapidly, as in April on the Pacific Coast or in September in New Mexico. Under such circumstances there usually is more variability than that indicated by the tabulation. Conversely, when the rainfall totals of the neighboring months on either side are about the same (for example, in March in central Oregon), the amount of variation is rather less than indicated, and the percentage of occurrences of "under half" and "over double" is therefore somewhat too high in the tabulation. As the tables show, there are considerable differences in the variability of rainfall in the West, with the greatest amount occurring in California and the least in the northern Rocky Mountains.

TABLE 2. Percentage of years in which the rainfall exceeds twice the normal for months having the normal rainfalls as shown.

Area numbers	Normal rainfall for month (inches)						
	0.5	1.0	1.5	2.0	2.5	3.0	4.0
2, 4, 11, 12, 14, 17, 20, 22, 23, 25	17	11	9	7	5	4	4
5, 8, 9, 10	15	17	16	15	12	11	11
15	15	13	13	12	12	11	11
16, 24	12	9	8	7	6	5	4
19, 15	9	8	7	6	5	4	3
26, 27	18	16	14	12	11	10	8

TABLE 3. Percentage of years in which the rainfall is less than half the normal for months having the normal rainfalls shown. These percentages include the months having no rainfall at all.

Area numbers	Normal rainfall for the month (inches)						
	0.5	1.0	1.5	2.0	2.5	3.0	4.0
2, 13, 16, 17, 20, 22	43	31	24	21	19	18	16
4	52	40	31	25	22	20	18
5, 8, 9, 10	63	50	43	40	36	35	33
11, 12	48	30	22	18	17	..	..
14	62	40	22	15	14	14	14
15, 19	28	25	22	20	20	19	18
23, 24	36	30	26	23	21	19	16
25, 26, 27	48	40	33	29	25	22	17

TABLE 4. Percentage of years in which there is no rainfall in month with normal rainfall as shown. (In this table "no rainfall" includes "trace" as used by the U. S. Weather Bureau.)

Area numbers	Normal rainfall for the month (inches)						
	0.5	1.0	1.5	2.0	2.5	3.0	4.0
2	8	4	2	1	0	0	0
4	13	6	2	0	0	0	0
5	45	30	20	13	9	6	3
8, 10	40	20	12	8	6	4	3
9	38	15	9	5	4	2	1
11, 12, 17	5	1	0	0	0	0	0
13	20	7	3	1	0	0	0
14, 22	10	4	1	0	0	0	0
15, 19	1	1	0.5	0	0	0	0
16, 24	3	1	0.5	0	0	0	0
20, 23	5	2	0.5	0	0	0	0
25	7	5	2	0	0	0	0
26	18	9	6	4	2	1	0
27	8	6	4	3	1	0	0

LITERATURE CITED

Alter, J. C. 1919. Normal precipitation in Utah. U. S. Monthly Weather Rev. **47**: 633-636.

Bates, C. G. 1924. Forest types in the central Rocky Mountains as affected by climate and soil. U. S. Dept. Agr. Dept. Bul. **1233**: 152 p.

Blake, D. 1933. Storm types and resultant precipitation in the San Diego area. U. S. Monthly Weather Rev. **61**: 223-224.

Clark, H. W. 1937. Association types in the north coast ranges of California. Ecology **18**: 214-230.

Clyde, G. D. 1931. Relationship between precipitation in valleys and on adjoining mountains in northern Utah. U. S. Monthly Weather Rev. **59**: 113-116.

Conroy, C. C. 1933. The relative distribution of early and late seasonal rainfall in southern California. U. S. Monthly Weather Rev. **61**: 14-15.

Cook, A. W. 1934. Marked summer air-mass displacements in California and their effects on the weather. U. S. Monthly Weather Rev. **62:** 39-45.

Dague, C. I. 1929. Low relative humidity in Oregon. U. S. Monthly Weather Rev. **57:** 146-153.

Fisher, L. C. 1934. Precipitation averages for the state of Washington as affected by habitability. U. S. Monthly Weather Rev. **62:** 241-243.

Gray, L. G. 1934. Long period fluctuations of some meteorological elements in relation to California forest-fire problems. U. S. Monthly Weather Rev. **62:** 231-235.

Haig, I. T., K. P. Davis, & R. H. Weidman. 1941. Natural regeneration in the western white pine type. U. S. Dept. Agr. Tech. Bul. **767:** 99 p.

Hart, F. C. 1937. Precipitation and run off in relation to altitude in the Rocky Mountain Region. Jour. Forestry **35:** 1005-1010.

Hayes, G. L. 1941. Influence of altitude and aspect on daily variation of factors of forest fire danger. U. S. Dept. Agr. Cir. **591:** 39 p.

Henry, A. J. 1919. Increase of precipitation with altitudes. U. S. Monthly Weather Rev. **47:** 33-41.

Krauch, H. 1939. Analysis of a 36-year record of precipitation at Cloudcroft, New Mexico. Southwestern Forest and Range Expt. Sta. Res. Note **60:** 5 p.

Larsen, J. A. 1922. Weather records at lookout stations in north Idaho. Jour. Forestry **20:** 215-219.

1925. The forest fire season at different elevations in Idaho. U. S. Monthly Weather Rev. **53:** 60-63.

1930. Forest types of the northern Rocky Mountain Region and their climatic controls. Ecology **11:** 631-672.

Larsen, J. A. & C. C. Delavan. 1922. Climate and forest fires in north Idaho. U. S. Monthly Weather Rev. **50:** 55-68.

Lee, C. H. 1911. Precipitation and altitude in the Sierra. U. S. Monthly Weather Rev. **39:** 1092-1099.

Little, D. M. 1931. Some effects of California mountain barriers on upper air winds and sea level isobars. U. S. Monthly Weather Rev. **59:** 376-380.

McAdie, A. 1914. The rainfall of California. Univ. Calif. Pubs., Geog. **1:** 127-140.

Merriam, W. B. 1936. Climate of the Rogue River Valley, Oregon. U. S. Monthly Weather Rev. **64:** 291-294.

Morris, W. G. 1934. Lightning storms and fires on the National Forests of Oregon and Washington. U. S. Monthly Weather Rev. **62:** 370-375.

Munger, T. T. 1925. Rainfall probability during the fire season in western Oregon and Washington. U. S. Monthly Weather Rev. **53:** 394-397.

Pearson, G. A. 1931. Forest types in the southwest as determined by climate and soil. U. S. Dept. Agr. Tech. Bul. **247:** 144 p.

Piper, C. V. & R. K. Beattie. 1915. Flora of the northwest coast. Press of the New Era Printing Co., Lancaster, Pa. 418 p.

Price, R. & R. B. Evans. 1937. Climate of the west front of the Wasatch Plateau in central Utah. U. S. Monthly Weather Rev. **65:** 291-301.

Robbins, W. W. 1937. Native vegetation and climate of Colorado in their relation to agriculture. Colo. Agr. Expt. Sta. Bul. **224:** 56 p.

Shepard, H. B. 1937. Forest fire insurance in the Pacific Coast states. U. S. Dept. Agr. Tech. Bul. **551:** 168 p.

Shreve, F. 1915. The vegetation of a desert mountain range as conditioned by climatic factors. Carnegie Inst. Wash., Pub. **217:** 112 p.

1927. The physical conditions of a coastal mountain range. Ecology **8:** 398-414.

Smith, G. E. P. 1910. Groundwater supply and irrigation in the Rillito Valley. Ariz. Agr. Expt. Sta. Bul. **64:** (81)-244 p.

Sprague, M. 1934. Monthly and seasonal distribution of snowfall in California. U. S. Monthly Weather Rev. **62:** 438-441.

U. S. Bureau of Agricultural Economics. 1936. Atlas American agriculture. U. S. Government Printing Office, Washington, D. C.

U. S. Department of Agriculture. 1941. Climate and man. U. S. Dept. Agr. Yearbook 1941: 1248 p.

U. S. Weather Bureau. Climatic summary of the United States. Washington, D. C.

Varney, B. M. 1920. Monthly variations of the precipitation-altitude relation in the central Sierra Nevada of California. U. S. Monthly Weather Rev. **48:** 648-650.

1925. Seasonal precipitation in California and its variability. U. S. Monthly Weather Rev. **53:** 148-163, 208-218.

Wells, E. L. 1922. Precipitation in Oregon. U. S. Monthly Weather Rev. **50:** 405-409.

the fire
U. S.

nwest as
gr. Tech.

e north-
Co., Lan-

the west
h. U. S.

imate of
lo. Agr.

e Pacific
: 168 p.

nountain
Carnegie

nountain

d irriga-
Sta. Bul.

ution of
her Rev.

. Atlas
Printing

ate and
8 p.

e United

the pre-
Sierra
her Rev.

and its
148-163,

. Month-